

## FOSSIL DECAPOD CRUSTACEANS FROM THE LATE OLIGOCENE TO EARLY MIOCENE PYSHT FORMATION AND LATE EOCENE QUIMPER SANDSTONE, OLYMPIC PENINSULA, WASHINGTON

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## ABSTRACT

Fossil decapod crustaceans of the Twin River Group, including the Hoko River, Makah, and Pysht formations, of the Olympic Peninsula, Washington, have received little systematic attention since Rathbun's work in 1926. The current study provides emended descriptions of several taxa that were previously described by Rathbun as occurring in rocks that are now referable to the Pysht Formation. Two new species are described from the Pysht Formation, *Trichopeltarion berglundorum* and *Asthenognathus cornishorum*. This marks the first notice of both *Trichopeltarion* and *Asthenognathus* on the west coast of North America. *Macrocheira longirostra*, new species from the late Eocene Quimper Sandstone, Olympic Peninsula, Washington, marks the earliest known occurrence of the genus *Macrocheira*, previously known from the Oligocene of Washington and the Miocene, Pliocene, and Recent of Japan. Decapod occurrences corroborate previously reported depths for the Pysht Formation, deposited in bathyal conditions that shallowed to inner sublittoral depths, and the Quimper Sandstone, deposited in littoral to sublittoral depths.

Decapods of the Pysht and Makah formations and the Quimper Sandstone are remarkably similar to Cenozoic decapods described from Japan. This evidence provides a biogeographic link between the east and west North Pacific decapod faunas that appears to have existed as early as the late Eocene. This link persists in the Recent because five genera from the Twin River Group and Quimper Sandstone are represented among extant decapods of the North Pacific Ocean.

KEY WORDS: Decapoda, Brachyura, Anomura, Oligocene, Miocene, Washington

## INTRODUCTION

This study describes several decapod taxa, including two new species collected from the late Oligocene to early Miocene Pysht Formation of the late Eocene to early Miocene Twin River Group and one new decapod species collected from the late Eocene Quimper Sandstone.

Fossil decapod crustaceans of the northwest coast of North America were originally described in the 19th and early 20th centuries by such workers as Dana (1849), Gabb (1864), Rathbun (1916, 1926), and Withers (1924). In 1926, Rathbun described several decapod taxa, some of which were collected from rocks that have since been assigned to the Twin River Group. Subsequently, decapod crustaceans of the Twin River Group, specifically the Pysht Formation, have received little additional systematic attention until recently. Lasmanis and Berglund (1991) figured taxa from the Pysht Formation. Feldmann et al. (1991) provided a general discussion of the decapod fauna of the Twin River Group, and Tucker (1995) conducted a comprehensive study of the Raninidae including those of the

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Twin River Group. Hopkins and Feldmann (1997) evaluated ctenochelids of the late Eocene to early Oligocene Makah Formation in the Twin River Group as well as the late Oligocene to early Miocene Pysht Formation.

The decapod fauna of the Pysht Formation is dominated in number of individuals by the ctenochelid *Callianopsis clallamensis* (Withers) but includes genera in several other families including the Callianassidae, Calappidae, Atelecyclidae, Portunidae, Majidae, and Pinnotheridae. In addition, the Pysht Formation has yielded an extremely large claw (CM 39690, deposited in the Carnegie Museum of Natural History) that is insufficiently complete to provide an identification or description. The Pysht Formation decapods differ from those of the other formations of the Twin River Group, the Hoko River and Makah formations. The Hoko River decapod fauna is dominated by raninids and goneplacids (Feldmann et al., 1991; Tucker, 1995). No species and only one genus, *Portunites* Bell, are shared between the Hoko River Formation and the Pysht Formation as far as is known. The Makah Formation and the Pysht Formation share the species *Callianopsis clallamensis*, but the two formations do not share any other species and only one other genus, *Portunites*. The decapod fauna of the Pysht Formation is remarkably similar to the Cenozoic, especially the early Miocene, decapod fauna from Japan (Karasawa, 1993; among others). Every decapod species herein identified from the Pysht Formation, with the exception of the callianassid taxa, has a Miocene congener in Japan.

Within this paper, several taxa originally named and described by Rathbun and others have been redescribed based upon the availability of more complete fossil material. Additionally, three new species have been recognized, and affinities with the Miocene Japanese decapod fauna are also discussed.

#### STRATIGRAPHY AND GEOLOGIC SETTING

The study area for the Twin River Group is located along the north coast of the Olympic Peninsula, Washington (Fig. 1). The Olympic Peninsula is composed of several terranes, some of which are considered to have been accreted, probably in the Paleocene to early Eocene, when the Kula and Farallon plates were moving obliquely northeast along the North American plate (Snively, 1987). These accreted rocks as well as some deep marine sediments and volcanics are believed to comprise most of the core rocks of the northern Olympic Peninsula (Babcock et al., 1994). The core complex consists of metamorphic rocks and turbidites with interbeds of basalt and is overlain by the Crescent "Terrane" (Fig. 1), which is primarily composed of autochthonous sedimentary rocks (Babcock et al., 1994). The Crescent "Terrane" is separated from the core rocks of the peninsula by faults.

The lowermost unit of the Crescent "Terrane" on the northern Olympic Coast is the Blue Mountain Unit, composed of early Eocene marine turbidite sediments thought to have been a submarine fan (Babcock et al., 1994). The Blue Mountain unit is overlain by the volcanic Crescent Formation, which is itself overlain by the marine Aldwell Formation, composed of siltstones, sandstones, and conglomerates (Babcock et al., 1994). The Eocene Aldwell Formation is believed to have been deposited in cold, deep water and to represent landslides or mudflows (Babcock et al., 1994). Overlying the Aldwell Formation is the late Eocene Lyre Formation (Snively, 1987), composed of breccias and sandstones deposited in shallow to deep water conditions (Babcock et al., 1994). Apparently the basin in



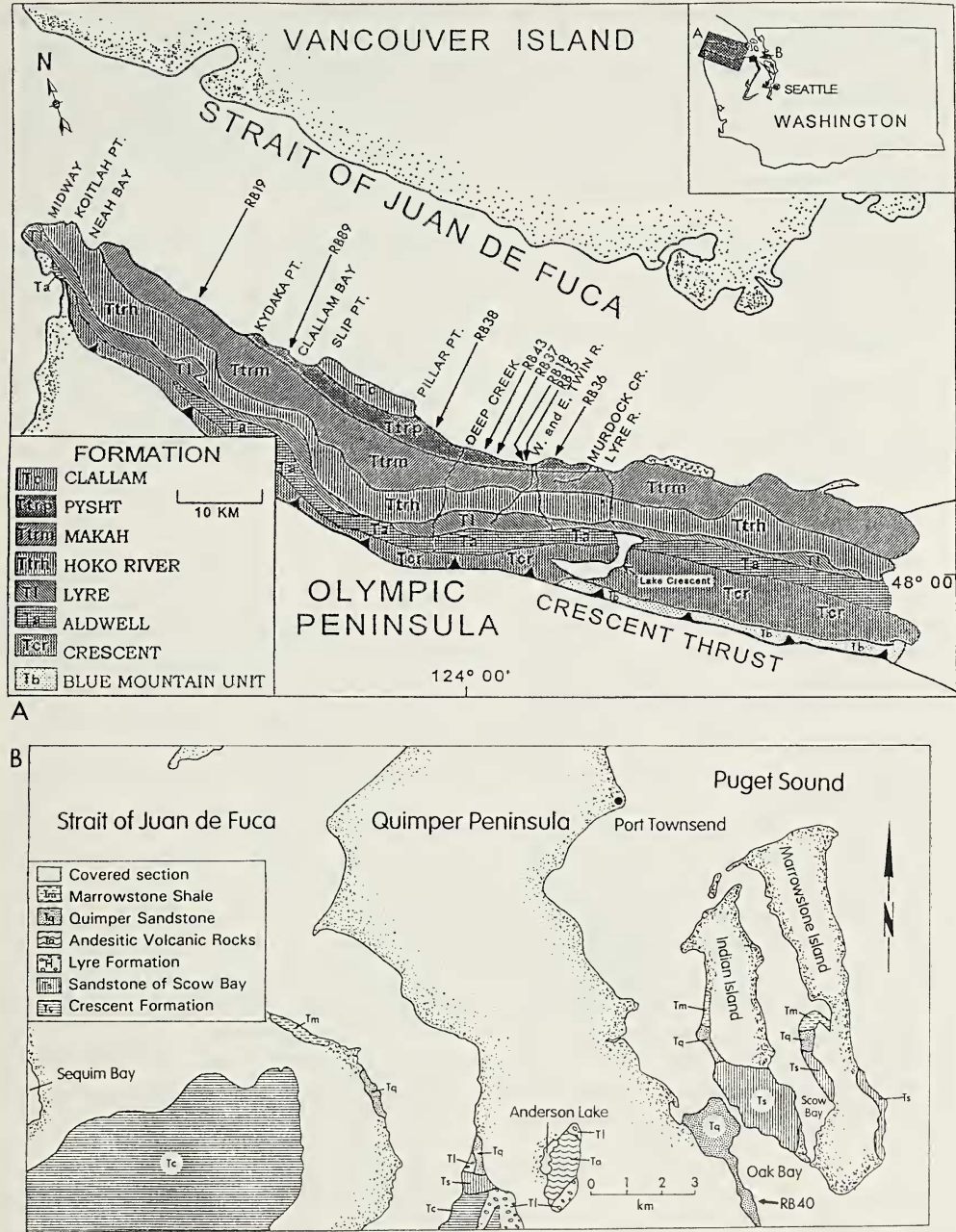


Fig. 1.—Map showing geology and collecting localities of the northern Olympic Peninsula, Washington. Enlarged area A depicts geology and collecting localities for the Twin River Group (map modified from Tucker [1995]). Enlarged area B depicts geology and collecting locality for the Quimper Sandstone (map modified from Armentrout and Berta [1977] and Babcock et al. [1994]).

which the Lyre Formation was being deposited deepened over the course of deposition (Babcock et al., 1994). Rapid subsidence was initiated in the late Eocene, and the Hoko River Formation was deposited in the deepening Tofino–Fuca basin paralleling the north coast of the Olympic Peninsula (Snively, 1987). The Makah Formation was deposited when this basin was at its deepest during the late Eocene to Oligocene, and the late Oligocene to early Miocene Pysht and the Miocene Clallam formations were deposited as this basin shallowed into the Miocene (Snively, 1987).

The Quimper Sandstone crops out on the Quimper Peninsula and Marrowstone and Indian islands which are located on the east coast of the Olympic Peninsula (Fig. 1). The Quimper Sandstone is underlain by the middle Eocene sandstones of Scow Bay which probably represent midfan channel fill deposits (Babcock et al., 1994). The Quimper Sandstone is separated from the Scow Bay sandstones by an angular unconformity in most areas, and in other areas, the Quimper Sandstone overlies the Lyre Formation (Babcock et al., 1994). The overlying Marrowstone Shale was deposited in a deep, rapidly subsiding basin (Babcock et al., 1994).

#### QUIMPER SANDSTONE

The Quimper Peninsula, located at the east end of the Olympic Peninsula, contains a section of Eocene marine sedimentary rocks (Fig. 2). Included in this sequence is the late Eocene Quimper Sandstone, believed to be approximately the same age as the Makah Formation (Babcock et al., 1994). The Quimper Sandstone has been assigned a Refugian age based upon molluscs and foraminifera (Armentrout and Berta, 1977). The lower part of the Quimper Sandstone contains amalgamated sandstone with crossbedding that indicates a shallow-water depositional environment while the upper part of the formation contains laminated siltstone and shale deposited below wave base (Babcock et al., 1994). The unit shows fining upward representing a deepening sequence from inner to outer shelf environments (Babcock et al., 1994). The provenance of this formation was likely Vancouver Island, the Coast Plutonic Complex, and the North Cascades (Babcock et al., 1994). Megafossils collected from the base of the Quimper Sandstone suggest that it was deposited on an inner shelf in littoral to sublittoral, warm temperate water conditions (Armentrout and Berta, 1977). Benthic foraminifera collected from the upper part of the formation indicate shelf deposition in sublittoral to upper bathyal, warm temperate water conditions (Armentrout and Berta, 1977). Material referred to *Macrocheira longirostra* was collected from locality RB40 in the Quimper Sandstone, located along the west shoreline of Oak Bay, south of Port Townsend, Washington (Fig. 1).

#### TWIN RIVER GROUP

##### Overview

The Twin River Group was originally named the Twin River Formation by Arnold and Hannibal (1913:584–585) who recognized it as a sequence of “soft clay shales and intercalated beds of sandstone” of late Oligocene and Miocene age that cropped out on the northern Olympic Peninsula along the Strait of Juan de Fuca from about five kilometers east of Twin Rivers to Pysht Bay. Arnold and Hannibal’s definition of the upper and lower contacts as well as the areal extent of the Twin River Formation was rather ill-defined and arbitrary. In 1958, Brown

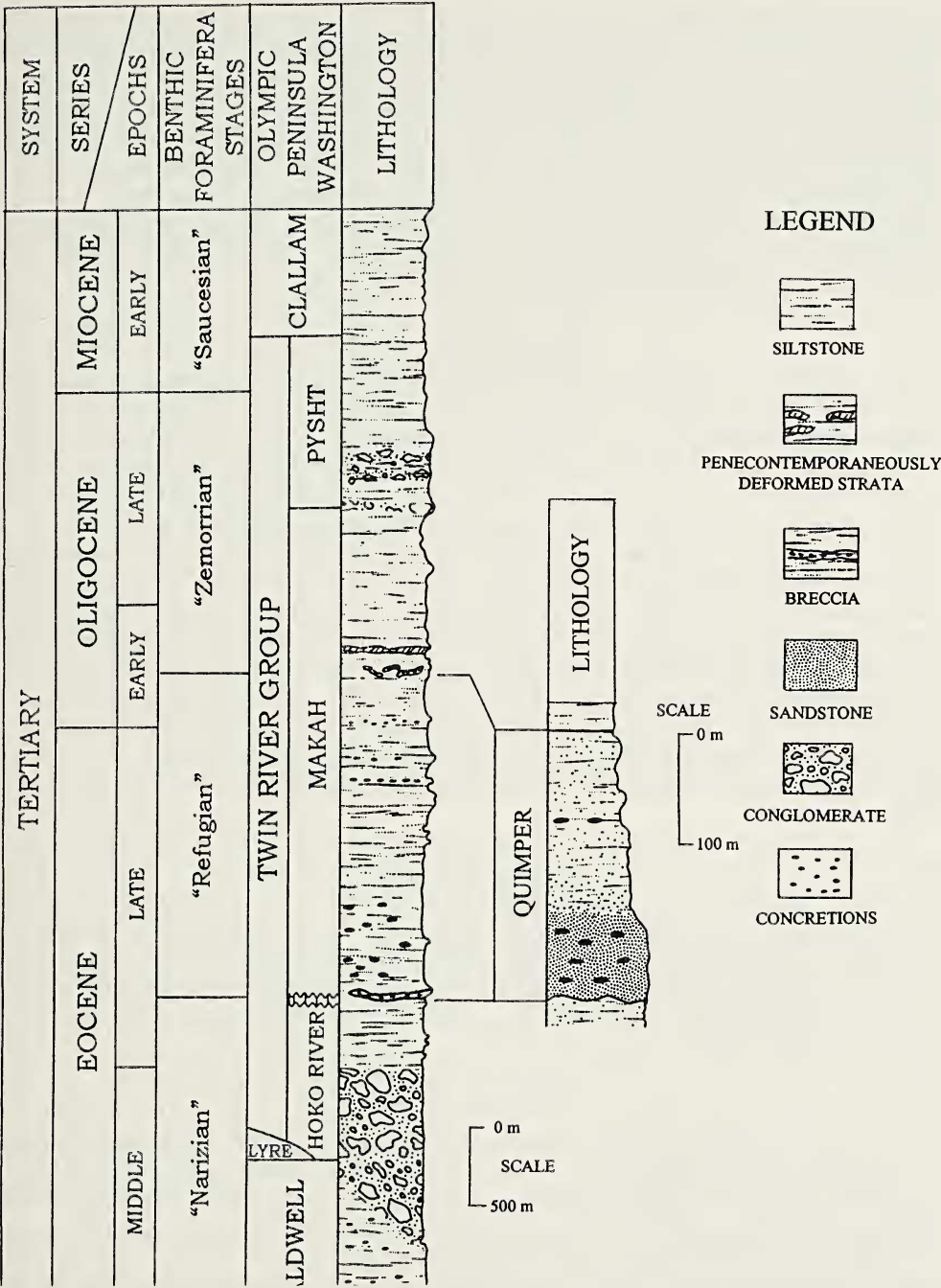


Fig. 2.—Generalized stratigraphic column of the Twin River Group and stratigraphic column of the Quimper Sandstone on West Marrowstone Island. Twin River Group column modified from Tucker (1995:370) and Quimper Sandstone column modified from Armentrout and Berta (1977:222).



and Gower redefined the formation to include up to 5300 m of sandstones, siltstones, and conglomeratic beds that extended from Clallam Bay to east of Port Angeles. The Twin River Formation was reported to overlies the Lyre Formation and to be conformably overlain by the Clallam Formation (Brown and Gower, 1958). Brown and Gower (1958) divided the Twin River Formation into three mappable members (lower, middle, and upper), and later, Snively et al. (1978) elevated each member to formation status, named each, and elevated the Twin River Formation to the Twin River Group (Fig. 2). They also extended the range of outcrop of the Twin River Group to include rocks extending from Neah Bay to east of Port Angeles (Snively et al., 1978).

### *Hoko River Formation*

The lowermost formation, the Hoko River Formation, is composed of massive- to thin-bedded siltstone and thinner beds of sandstones and conglomerates and ranges from 1600–2300 m in thickness (Snively et al., 1978). Calcareous concretions have been collected throughout the Hoko River Formation, and they often contain decapods, gastropods, and wood fragments as their nuclei (Snively et al., 1978). The Hoko River Formation conformably overlies the Lyre Formation and intertongues with it at some localities (Snively et al., 1978). It is conformably overlain by the Makah Formation, the middle unit of the Twin River Group, in most localities but in some areas there is an unconformity between the two formations (Snively et al., 1978). The Hoko River Formation is believed to be late Eocene (late Narizian Stage of Mallory) in age, based upon molluscan and foraminiferan assemblages (Snively et al., 1978). Addicott (*in* Snively et al., 1978) believed that crab occurrences placed the Hoko River Formation in the late Eocene, but Tucker (1995) reported that crab-bearing concretions were probably formed before their final deposition, making them somewhat older than the Hoko River sediments.

The depositional environment of the Hoko River Formation is thought to have been relatively deep and cool according to foraminiferal data (Rau, 1964). Depths may have ranged from bathyal to sublittoral, and the depth is estimated to have been 90–300 m (Rau, 1964). The Hoko River Formation is believed to have been deposited in a shallower environment than the Makah Formation, the middle unit of the Twin River Group, and much of the Pysht Formation, the uppermost unit of the Twin River Group, based on foraminiferal assemblages recovered from each unit (Rau, 1964).

### *Makah Formation*

The middle formation of the Twin River Group, the Makah Formation, is composed chiefly of thin-bedded siltstone and turbiditic sandstone and includes six mappable members of differing lithologies (Snively et al., 1978). The bulk of the formation is composed of siltstone beds ranging in thickness from one to ten centimeters interbedded with sandstones that display typical Bouma turbidite sequences (Snively et al., 1980). The Makah Formation achieves an average thickness of 2800 m and is believed to be late Eocene to Oligocene in age based upon foraminiferal assemblages (Snively et al., 1980).

Mappable members of the Makah Formation include four thick-bedded, turbiditic sandstones, an olistostromal unit of shallow-marine sandstone, and a bed of water-lain tuff (Snively et al., 1978). Calcareous concretions may be found

throughout the Makah Formation and these contain nuclei of calcite crystals, decapods, plant fragments, and worm burrows (Snaveley et al., 1980). One of the mappable members of the Makah Formation, the olistostromal Jansen Creek Member, lies near the middle of the Makah Formation. It is believed to be an allocthonous unit resulting from erosion of uplifted, older rocks that bordered the deep marginal basin where the Makah Formation was being deposited (Snaveley et al., 1980). The Jansen Creek Member is composed of shallow water conglomerate and fossiliferous sandstone and is enclosed by younger deepwater deposits according to foraminiferal data (Snaveley et al., 1980). Snaveley et al. (1978) believed the Jansen Creek Member to be late Eocene in age based upon molluscs and foraminifera and to be overlain by beds of Zemorrian Age (Oligocene). However, Squires and Goedert (1994) reported the Jansen Creek Member to be earliest Oligocene in age (p. 402). The fauna of this member represents a bathyal assemblage (Squires and Goedert, 1994). The Jansen Creek Member contains numerous fossiliferous calcareous concretions and contains the vast majority of the decapods found in the Makah Formation. The ctenochelid species *Callianopsis clallamensis* was collected from this unit.

Because the Makah Formation contains turbiditic sandstones, it is believed to represent a rapidly deposited submarine fan in the marginal Tofino–Fuca basin (Snaveley et al., 1980). The Tofino–Fuca basin is thought to have been at its deepest during the late Eocene to Oligocene, when the Makah Formation was being deposited (Snaveley et al., 1980:24). This interpretation is strengthened by the fact that foraminifera collected from the Makah Formation suggest a lower to middle bathyal, open water environment (Snaveley et al., 1980:21). Rau (1964) believed the middle member of the Twin River Formation (Makah equivalent) to have been deposited at bathyal depths from 300–1830 m based on foraminiferal assemblages, which supports the interpretation of the Makah Formation as a deep basin deposit.

### *Pysht Formation*

The Pysht Formation is the uppermost formation assigned to the Twin River Group. Every taxon herein described except *Macrocheira longirostra* was collected from the Pysht Formation. Unfortunately, the lithology and the stratigraphy of the Pysht Formation have not received comprehensive descriptive attention. Brown and Gower (1958) briefly described the lithology of the Twin River Formation and designated lower, middle, and upper members, of which the Pysht Formation is the upper member. They reported that the unit was composed chiefly of thin-bedded to massive, poorly indurated gray siltstones with occasional interbedded sandstones, and subsequent workers have concurred with this description for most of the Pysht Formation section (Rau, 1964; Addicott, 1976; Snaveley et al., 1978; Armato, 1993; Squires and Goedert, 1994; Tucker, 1995). In addition to the work of Brown and Gower (1958), brief and/or limited lithologic and stratigraphic descriptions of the Pysht Formation have been provided by Rau (1964), Addicott (1976), Snaveley et al., (1978), Snaveley (1983), and Squires and Goedert (1994). An accurate thickness of the unit has yet to be determined due to structural complications, but it is estimated to be about 1100–1400 m thick (Snaveley et al., 1978). The underlying Makah Formation has a gradational contact with the Pysht Formation in some areas but is unconformable in others (Snaveley,



1983). The upper contact between the Pysht Formation and the Clallam Formation is gradational and conformable (Snively et al., 1978).

Completion of detailed stratigraphic and lithologic descriptions of the Pysht Formation are hampered by several factors. First, there are structural complications in the area of outcrop. Numerous faults extend both north-south and east-west throughout the Pysht Formation (see Tabor and Cady, 1978). Second, much of the Pysht Formation section is covered by dense vegetation with occasional outcrops along the Strait of Juan de Fuca and streams, making it difficult to correlate between outcrops or even observe the rocks in many areas. Third, the Pysht Formation is composed of sandy siltstone and siltstone with interbedded sandstones throughout most of its vast thickness, and the occasional conglomerates appear to be similar in lithology. This monotonous and repetitive lithology with a lack of reliable key marker beds makes it difficult to correlate between localities.

Details of the stratigraphy and lithology of the Pysht Formation, beyond a general description, presented by various workers are brief and at times contradictory. Rau (1964) provided a lithologic description of each member of what was then known as the Twin River Formation. He described the probable ecologic setting of the depositional environment of the upper part of the upper member of the Twin River Group (= upper Pysht Formation) which he believed to have been deposited in cool, relatively deep waters that shallowed considerably near the top of the formation (Rau, 1964).

Addicott (1976) collected molluscs from what he believed to be the upper 400–500 m of the upper member of the Twin River Formation (= Pysht Formation), consisting of siltstone and sandy siltstone with an interbedded lens of fossiliferous conglomerate. He reported that the fossiliferous conglomerate unit was exposed on a ridge south of Pearson Creek which is located between Slip Point and Pillar Point and that other exposures occurred at Pillar Point State Recreational Area and localities near Sekiu at the west end of Clallam Bay (Addicott, 1976). Gower (*in* Addicott, 1976) had mapped the conglomerate as being located in the lower part of the Clallam Formation, but Addicott (1976) reported that this conglomerate occurred about 1000 m above the base of the Pysht Formation. He assigned an early Miocene age based upon molluscan assemblages to the conglomerate and to overlying sandstones and siltstones of the upper 30–40 m.

Subsequently, Snively et al. (1978) reported that conglomeratic channels occurred at the base of the Pysht Formation and that they were interbedded with siltstone and sandstone of the Makah Formation (Snively et al., 1978). These conglomerate beds were observed along the coast between Sekiu and Kydaka Point and were reported to be composed of reworked cobble- and boulder-sized clasts of metamorphic and igneous rocks, felsic tuff, and mollusc-bearing sandstone (Snively et al., 1978). These boulders are believed to have been derived from nearly lithified strata of approximately the same age located on Vancouver Island (Snively et al., 1978). Snively et al. (1978:A118) proposed that these conglomerates were similar to those located in the “western part of the Pysht Quadrangle.” The conglomerates of the “western part of the Pysht Quadrangle” are the same conglomerates that Addicott (1976) believed to be located 1000 m above the base of Pysht Formation. Because of the lithologic similarity between the conglomerates of the Sekiu-Kydaka Point area which mark the basal contact of the Pysht and those of the “western part of the Pysht Quadrangle,” Snively et al. (1978) proposed that all of the conglomerates must indicate the base of



Pysht Formation. Oddly, they did not discuss the discrepancy between this conclusion and that of Addicott (1976), who placed the conglomerate of the "western part of the Pysht Quadrangle" 1000 m above the base of the Pysht Formation. Snively et al. (1978) assigned the Pysht Formation a late Oligocene to early Miocene age based upon foraminifers and molluscs.

Armato (1993) reported that the base of the Pysht Formation was composed of conglomerate interbedded with siltstones of the upper Makah Formation. He did not report a conglomeratic unit to be located in the upper portion of the formation that could correspond to the conglomerate reported by Addicott (1976). However, Armato (1993) used the stratigraphic column of the Pysht Formation provided by Addicott (1976), which illustrates the conglomerate 1000 m from the base of the Pysht Formation but does not depict conglomerate at the base of the Pysht section.

In 1994, Squires and Goedert reported that the lower part of the Pysht Formation, just west of the mouth of Murdock Creek, was composed of mudstone with small, discontinuous sandstones at the localities they sampled. They assigned the lower Pysht Formation to the latest early or earliest late Oligocene, based upon the presence of gastropods transitional in morphology between *Liracassis rex* (Tegland) and *L. apta* (Tegland).

We are unable to provide a satisfactory solution to the question of the position of the conglomerate bed or beds in the Pysht Formation. At least two possibilities exist. One solution is that there is more than one conglomerate bed, with one (or more) near the base of the formation and one about 1000 m above the base. Obviously the other solution is that there is only one conglomerate bed near the base of the formation. Conglomeratic float observed by one of us at locality RB36 contained sedimentary concretions similar to those found in the siltstone layers and igneous clasts including granites. The RB36 locality is not located near any of the previously discussed conglomerate localities, so it is possible that this conglomeratic float represents still another conglomerate bed. However, since the conglomerate was observed as float, it is uncertain as to exactly where in the section it originated.

Another problem with the discrepancy of the conglomerate beds lies in the age determination. Addicott (1976) assigned the conglomerate he studied to the early Miocene; Snively et al. (1978) appear to believe that this same conglomerate lies at the base of the formation. Squires and Goedert (1994) determined that localities near the base of the Pysht Formation just west of Murdock Creek were latest early or earliest late Oligocene in age. If the conglomerate described by Snively et al. (1978) and Addicott (1976) is indeed the same bed and is located near the base, this creates a disturbing age discrepancy with two possible ages for the base of the formation. More detailed mapping, stratigraphic work, and collection of age-diagnostic fossils, all of which is beyond the scope of this study, will be necessary to resolve these discrepancies.

It is the opinion of the authors at the present time that there is most likely more than one conglomerate bed, with at least one being located near the contact with the Makah Formation at the base of the Pysht and one occurring near the top of the formation 1000 m above the base. This conclusion seems warranted for several reasons. First, based upon lithologic similarity only, Snively et al. (1978) generalized that all of the conglomerates of the Pysht Formation must be located at the base; however, more convincing evidence, namely fossils, would be necessary to demonstrate that all of the conglomerates indeed represent the same bed. Second, because the conglomerate of Addicott was assigned an early Miocene age,

it is more likely to be located near the top of the formation since the overlying Clallam Formation, with which the Pysht is conformable, is late early Miocene in age (Addicott, 1976). Third, the underlying Makah Formation is considered to be late Eocene to late Oligocene in age based upon foraminiferans (Snively et al., 1980). Squires and Goedert (1994) reported that the lower Pysht Formation was latest early to earliest late Oligocene in age. This age determination for the base of the Pysht Formation is more consistent with the age reported for the Makah Formation than is an early Miocene age, especially because the Pysht and Makah formations are in many places conformable. Fourth, some of the outcrops sampled by Addicott (1976) are geographically near the contact between the Pysht Formation and the Clallam Formation, making it more likely that the conglomerate he sampled was near the top of the Pysht section unless faults or other structural complications exist near those localities.

The Pysht Formation contains the most diverse fauna of any of the formations of the Twin River Group (Feldmann et al., 1991). Megafossils include pelecypods, gastropods, scaphopods, pteropods, the nautiloid *Aturia* Bronn, the isopod *Bathynomus goedertorum* (Wieder and Feldmann), wood bored by *Teredo* Linnaeus, scleractinian corals, bryozoans, decapods, and vertebrates including cetaceans, a bird, and the shark *Hepranchias howelli* (Reed) (Weaver, 1942; Addicott, 1976; Olson, 1980; Kaler, 1989; Squires, 1989; Wieder and Feldmann, 1989; Feldmann et al., 1991; Squires and Goedert, 1994).

The age of the Pysht Formation is believed to be latest early or earliest late Oligocene (Zemmorian Stage) to early Miocene (Saucesian Stage) in age based on foraminiferans (Snively, 1983) and molluscs (Addicott, 1976; Squires and Goedert, 1994). Addicott (1976) believed the upper 400–500 m of the Pysht Formation to be early Miocene in age, and he assigned the mollusc assemblage from this part of the section to the *Echinophoria apta* faunal zone, even though *Liracassis apta* (= *Echinophoria*) itself was not known to occur there at the time of his study. *Liracassis apta* has been recovered from some localities of the Pysht Formation, including the exposures at RB18 and RB36 which are relatively close stratigraphically to locality A3678 of Addicott (1976). Locality A3678 is stratigraphically lower than the portion of the Pysht Formation assigned by Addicott (1976) to the early Miocene.

The Pysht Formation is interpreted to have been initially deposited in cool waters, approximately 300–1830 m deep, based on the foraminiferal assemblage collected from the lower portion of the upper member of the Twin River Formation (= Pysht) (Rau, 1964). Armato (1993) reported that the depositional environment near the central part of the Pysht Formation section was characterized by moderately deep sublittoral to bathyal depths and cool water temperatures, based on molluscan assemblages. The upper part of the Pysht Formation represents shallower but cool waters, probably inner sublittoral in depth, based upon foraminiferans (Rau, 1964) and molluscs (Armato, 1993). Addicott (1976) believed the upper part of the upper member of the Twin River Formation (= Pysht) to have been deposited in relatively shallow water, in part because of the absence of the deep-water genus *Liracassis*. Rau (1964) reported that the shallowing of the upper portion of the Pysht Formation represented a regional shallowing event that continued during deposition of the Miocene Clallam Formation, a sandy and conglomeratic formation interbedded with coal deposits (Addicott, 1976).



Table 1.—*Decapod collecting localities within the Twin River Group and Quimper Sandstone. Locality numbers are from the locality register of Ross Berglund. More detailed locality descriptions are given in the text.*

Locality numbers	Description of localities
RB15	Pysht Formation, W 1/2, Sec. 23, T31N, R10W, Twin River Quadrangle, 7.5' series, Clallam County, Washington.
RB18	Pysht Formation, SW 1/4, Sec. 23, T31N, R10W, Twin River Quadrangle, 7.5' series, Clallam County, Washington.
RB19	Makah Formation, SE 1/4, SE 1/4, Sec. 26, T33N, R14W of the Clallam Bay Quadrangle, 15' series, Clallam County, Washington.
RB36	Pysht Formation, SE 1/4, Sec. 23, T31N, R10W, Twin River Quadrangle, 7.5' series, Clallam County, Washington.
RB37	Pysht Formation, SW 1/4, NE 1/4, Sec. 21, T31N, R10W, Twin River Quadrangle, 7.5' series, Clallam County, Washington.
RB38	Pysht Formation, NE 1/4, SE 1/4, Sec. 13, T31N, R11W, Pysht Quadrangle, 7.5' series, Clallam County, Washington.
RB40	Quimper Sandstone, SW 1/4, NE 1/4, Sec. 18, T29N, R7E, Nordland Quadrangle, 7.5' series, E. Jefferson County, Washington.
RB43	Pysht Formation, NE 1/4, NW 1/4, Sec. 21, T31N, R10W, Twin River Quadrangle, 7.5' series, Clallam County, Washington.
RB89	Pysht Formation, N 1/2, SW 1/4, Sec. 18, T32N, R12W, Clallam Bay Quadrangle, 7.5' series, Clallam County, Washington.

#### TWIN RIVER GROUP LOCALITIES

Although it is certain that the decapods were collected from rocks referable to the Pysht Formation, stratigraphic assignment of the collecting localities (Table 1) within the Pysht Formation section is tentative because of the problems discussed. Decapods were collected from seven localities of the Pysht Formation (Fig. 1). Six of the localities occur along an approximately ten-kilometer section of the coast of the Strait of Juan de Fuca, and five of these localities crop out along approximately five kilometers of coast (Fig. 1). These six localities appear to be stratigraphically lower than the conglomerate described by Addicott (1976) as occurring about 400–500 km below the top of the Pysht Formation. The stratigraphic position of the seventh collecting locality is unknown.

Of the six easternmost localities, locality RB38 seems to be highest and RB36 to be lowest stratigraphically. Of these, RB37, RB38, and RB43 appear to be located stratigraphically higher than Addicott's A3678 locality and lower than his fossiliferous conglomerate. Localities RB15, RB18, and RB36 are believed to be very near locality A3678 of Addicott (1976). If the localities are indeed in these positions of the stratigraphic column relative to Addicott's localities, then the depositional environment of these six localities would correspond most closely to that described by Armato (1993) for the central part of the section. The age of the central part of the section appears to be late Oligocene based upon the work of Rau (1964), Addicott (1976), and Squires and Goedert (1994). The seventh and westernmost decapod collecting locality, RB89, crops out near Sekiu Point at the west end of Clallam Bay. The stratigraphic position, depositional environment, and relative age within the Pysht Formation of RB89 are unknown. According to Addicott (1976), this locality would be found in the upper conglomerate 1000 m from the base and, according to Snively et al. (1978), would be located in the basal conglomerate near the contact with the Makah Formation.

At the RB15 locality, decapods were collected in concretions as float in the



intertidal zone along the Strait of Juan de Fuca between the mouth of West Twin River and the loading dock of the West Twin Shale Quarry. A specimen of *Trichopeltarion berglundorum* n. sp. was collected in a concretion from this locality. The closely associated RB18 locality is located on an open hilltop overlooking the Strait of Juan de Fuca at the West Twin Shale Quarry. Fossils were collected as float in large expanses of quarried sandy siltstones and siltstones. This locality has yielded a decapod fauna dominated by *Callianopsis clallamensis* but includes *Trichopeltarion berglundorum*, *Mursia marcusana* Rathbun, *Macrocheira teglandi* Rathbun, *Asthenognathus cornishorum*, and possibly *Portunites triangulum* Rathbun. Associated fauna includes the gastropod *Liracassis apta*; the pelecypods *Acila gettysburgensis* (Reagan), *Portlandia* sp., *Archarax dalli* (Clark), *Thyasira* sp., *Macoma twinensis* Clark, *Modiolus* sp., and *Lucinoma acutilineata* (Conrad); scleractinian coral; vertebrate bone fragments; an echinoderm; *Teredo*-bored wood; and plant material. Most specimens were collected from concretions originating from medium- to thick-bedded siltstone blocks, but many were collected directly from the siltstone matrix.

At the Tegland Point locality (RB36), about 0.4 km east of the mouth of the East Twin River, fossils were collected along the Strait of Juan de Fuca from concretions occurring as float on a wave-cut terrace, and some concretions were collected in place from siltstone cliffs. Decapods from this locality include *Portunites triangulum*, *Mursia marcusana*, *Asthenognathus cornishorum*, and possibly *Macrocheira teglandi*. Associated fauna includes the gastropod *Liracassis apta*; the pelecypods *Katherinella etheringtoni* (Tegland), *Nucula* sp., *Portlandia* sp., *Archarax dalli*, and *Macoma twinensis*; and *Teredo*-bored wood.

Site RB37, located along the Strait of Juan de Fuca in the intertidal zone, yielded a large block of thin-bedded siltstone which occurred as float. This block contained large quantities of organic material on its bedding planes that included juvenile and adult decapods, molluscs, and large quantities of plant remains. Decapods recovered include *Portunites triangulum*, *Mursia marcusana*, *Macrocheira teglandi*, and *Asthenognathus cornishorum*.

Site RB38 is located in the intertidal zone along the Strait of Juan de Fuca east of the Silverking Fishing Resort near the mouth of Joe Creek. Decapods recovered from this locality include *Callianopsis clallamensis*, *Mursia marcusana*, and *Macrocheira teglandi*. Locality RB43, located along the Strait of Juan de Fuca approximately 3.0 km west-northwest of RB18 and about 0.60 km northwest of RB37, yielded one specimen of *Portunites triangulum*. Finally, one specimen of *Mursia marcusana* has been reported by amateurs from RB89 located at Sekiu Point at the west end of Clallam Bay; however, this specimen was not observed by the authors.

Locality RB19, the only locality from the late Eocene to Oligocene Makah Formation, is located at the mouth of Jansen Creek along the Strait of Juan de Fuca. It occurs in the Jansen Creek Member, an olistostromal unit believed to be somewhat older than the surrounding Makah Formation sediments, and yielded specimens of *Callianopsis clallamensis* preserved in concretions.

#### ABBREVIATIONS

The following abbreviations are used within the text of this paper: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; USNM, United States National Museum, Washington, D.C.; RB, Collecting localities in the lo-

cality register of Ross Berglund, Bainbridge Island, Washington; H, Height (where there are more than one height dimension listed, they are denoted by numbers and explained where relevant); L, Length (numbers are used as for height); W, Width (numbers are used as for height). All other abbreviations are explained in the text where appropriate.

#### SYSTEMATIC PALEONTOLOGY

##### Order Decapoda Latreille, 1803

##### Infraorder Anomura H. Milne Edwards, 1832

##### Superfamily Thalassinioidea Latreille, 1831

*Remarks.*—As has been discussed by Hopkins and Feldmann (1997), identification and interpretation of fossil members of the Thalassinioidea, within both the Callianassidae Dana, 1852, and the Ctenochelidae Manning and Felder, 1991, have historically been hindered by the nature of preservation of fossil material. Because of the delicate nature of most of the cuticle, fossil thalassinoids are largely represented by isolated claws and fingers. Unfortunately, the diagnostic characters of extant taxa, including the nature of the pleopods, details of carapace architecture, and form of the abdomen, are not usually available for study in fossil specimens. The recent revision of the callianassids by Manning and Felder (1991), however, provided several morphological characters of the first pereopods which, for the first time, permit recognition of more realistic relationships between fossil and recent taxa. Their clarification of the key characters necessary for recognition of genera has stimulated reassessment of several fossil taxa.

The two thalassinoid taxa described herein, *Callianassa* sensu lato cf. *C. porterensis* and *Callianassa* sensu lato sp. 1, do not possess sufficiently well-preserved material to permit referral to known taxa within the framework of Manning and Felder's (1991) revision.

##### Family Callianassidae? Dana, 1852

*Diagnosis.*—See Manning and Felder (1991).

*Remarks.*—In 1991, Manning and Felder revised the superfamily Thalassinioidea to include the Callianassidae Dana and the Ctenochelidae Manning and Felder, 1991. The two subfamilies are differentiated based upon characters not often preserved in the fossil record. The Ctenochelidae possess a cardiac prominence on the dorsal carapace and an appendix on the second pleopods of males. The uropodal exopod is longitudinally carinate on the dorsal surface and lacks a dorsal plate. The Callianassidae lack a cardiac prominence, appendix interna on the male second pleopods, and longitudinal dorsal keel on the uropodal exopods, and possess a dorsal plate on the uropods. None of these characters is preserved in the first two thalassinoid taxa herein described, the material for which consists only of portions of chelipeds. Nevertheless, they are assigned with some reservation to the Callianassidae because the cheliped material does not resemble that of species of any of the six genera assigned to the Ctenochelidae. Some members of the Ctenochelidae, such as *Ctenocheles* Kishinouye and *Dawsonius* Manning and Felder, have very distinctive major chelipeds. Additionally, two of the six genera of the Ctenochelidae are monotypic, including *Dawsonius* and *Paracalliax* de Saint Laurent (Manning and Felder, 1991), and the genus *Callianopsis* de Saint Laurent has few species, indicating that this family is less speciose and diverse than many genera of the Callianassidae. There are no ctenochelids besides *Cal-*



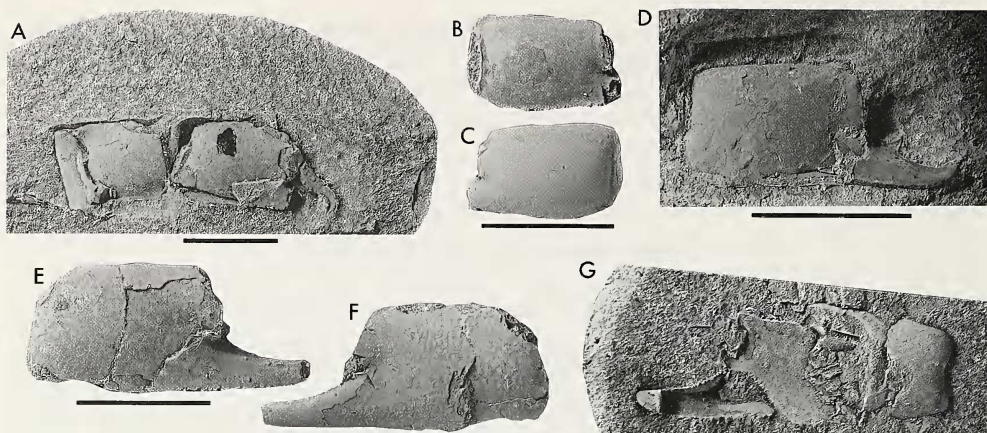


Fig. 3.—A. View of inner surface of cheliped of *Callianassa* cf. *C. porterensis*, CM 39654. B. Inner surface of manus of *Callianassa* cf. *C. porterensis*, CM 39655. C. Outer surface of manus of *Callianassa* cf. *C. porterensis*, CM 39655. D. Inner surface of manus of *Callianassa* sensu lato sp. 1, CM 39660. E. Inner surface of manus of *Callianassa* cf. *C. porterensis*, CM 39656. F. Outer surface of manus of *Callianassa* cf. *C. porterensis*, CM 39656. G. Outer surface of cheliped of *Callianassa* cf. *C. porterensis*, CM 39657. Scale bars = 1 cm. B/C and E/F share scales.

*lianopsis* found today on the North American coast of the Pacific Ocean (Manning and Felder, 1991). Callianassid genera found today in the eastern Pacific include *Neotrypaea* Manning and Felder, *Notiax* Manning and Felder, *Callichirus* Stimpson, *Corallianassa* Manning, *Glypturus* Stimpson, *Lepidophthalmus* Holmes, and *Cheramus* Bate (Manning and Felder, 1991). All of these factors suggest that the fossil material is most likely referable to a genus of the Callianassidae; however, better-preserved and more-complete material is necessary to confidently assign these specimens to a family and genus.

*Callianassa sensu lato*  
cf. *Callianassa porterensis* Rathbun, 1926  
(Fig. 3A–C, E–G)

*Callianassa porterensis* Rathbun, 1926:119.

**Diagnosis.**—Callianassid with manus of cheliped nearly twice as long as high, widening towards proximal margin, distal margin with elongate, serrated projection and indentation just below serrations; fixed finger with serrated upper margin; movable finger with serrate occlusal surface and strongly curved tip (modified from Rathbun, 1926).

**Description.**—Merus longer than high, upper margin straight, proximal margin broken, distal margin rounded, lower margin nearly straight, broken at proximal end. Carpus of cheliped about as long as high; inner surface slightly convex; proximal margin with triangular, blunt projection at articulation with merus, concave just below projection and curving convexly to lowest extent of margin; upper margin broken; lower margin straight, rimmed; distal margin broken on upper and lower corners but remainder straight.

Manus of cheliped longer than high, widening posteriorly, outer surface smooth; proximal margin rimmed, slightly convex; upper margin straight, sharp; lower margin straight, serrate; outer surface convex longitudinally and transversely; distal margin sinuous, extending slightly obliquely from upper margin to lower margin. Inflated region paralleling distal margin, margin incurved just below inflated region; fixed finger narrowing distally, finely serrate on both upper and lower margins, possessing a



Table 2.—Measurements (in mm) taken on the manus of specimens of *Callianassa sensu lato* cf. *C. porterensis*. L1 = maximum length, H1 = maximum height, L2 = length of fixed finger.

Specimen	L1	H1	L2	Locality
CM39655	14.6	7.1	—	RB36
CM39658	15.6	8.5	> 5.7	RB36
CM39656	21.0	> 9.4	> 7.8	RB36
CM39657	18.2	7.5	6.7	RB18
CM39654	>11.2	7.4	—	RB36

few scattered punctae; movable finger with finely serrate occlusal surface, wide proximally and narrowing distally, inner surface with two rows of small tubercles, distal tip strongly recurved to parallel distal margin of manus.

Inner surface of manus flattened on margins but convex centrally, smooth. Inner surface of fixed finger smooth, sometimes possessing a few small scattered tubercles, weakly developed keel extending from indentation in distal margin along fixed finger, appearing to disappear about two-thirds of the distance along the finger; upper surface of fixed finger serrated.

Remainder of animal unknown.

**Measurements.**—Measurements (in millimeters) taken on the manus of six specimens of *Callianassa sensu lato* cf. *Callianassa porterensis* are listed in Table 2. CM 39654: carpus, H (maximum) = 8.3, L (maximum) = 7.8; manus, H (maximum) = 2.8, L (maximum) > 7.8.

**Referred Specimens.**—Six specimens (CM 39654–39659) are deposited in the Carnegie Museum of Natural History.

**Localities and Stratigraphic Position.**—All of the specimens were collected as float in concretions along wave-cut terraces and shore cliffs of the Pysht Formation. CM 39654–39656 and CM 39658 and 39659 were recovered from RB36, and CM 39657 was collected from RB18.

**Remarks.**—Each of the six specimens referred to *Callianassa sensu lato* cf. *C. porterensis* was found in a concretion and consists of the manus of a cheliped. It is unknown as to whether they are major or minor chelae, and the incomplete nature of the material makes it impossible to assign it to a genus other than *Callianassa sensu lato*. Numerous similarities between the material described herein and *Callianassa porterensis* Rathbun permit tentative referral of the specimens to *C. porterensis*; however, the few discrepancies listed below do not allow the specimens to be assigned to that species with confidence.

The specimens described herein possess a manus that is longer than high, and higher proximally than distally, which is characteristic of *C. porterensis*. One specimen possesses a fixed finger with a serrated upper margin, another diagnostic character of *C. porterensis*. Rathbun's (1926) specimens were reported to be thicker near the proximal end of the manus and to have a smooth outer surface of the manus, true of the specimens studied herein. She also reported the presence of a few oblong tubercles on the outer surface of the manus in *C. porterensis* (Rathbun, 1926); the tubercles were not observed in this study. The inflated projection reported by Rathbun (1926) on the distal margin was serrated; in the specimens described herein the projection is not serrated.

Specimen CM 39654 is provisionally assigned to *Callianassa* cf. *C. porterensis*. CM 39654 possesses a movable finger, while the material assigned by Rathbun (1926) to *C. porterensis* does not, and Rathbun's (1926) material possesses the fixed finger while CM 39654 does not, making direct comparisons between the

new specimen and Rathbun's material difficult. However, the manus of CM 39654 and specimens referred to *C. porterensis* are similarly shaped and both possess a shallow indentation in the distal margin just above the position of the fixed finger. Both possess a serrated lower margin of the manus. Because of the presence of the serrated lower margin in both CM 39654 and specimens referred by Rathbun (1926) to *C. porterensis*, which is a unique character among the thalassinoid specimens from the Pysht Formation, CM 39654 is provisionally assigned to *Callianassa* cf. *C. porterensis*. The description of *C. porterensis* will need to be broadened if it becomes clear that the specimens described here may all be assigned confidently to *C. porterensis*.

Characters of CM 39654, the most complete specimen referred to *Callianassa* cf. *C. porterensis*, may be compared with characters for species of several recent genera. Species of the genus *Callichirus* Stimpson are characterized by a strongly curved tip on the movable finger, but the carpus is much longer than the manus, a condition not seen in CM 39654. Species of the genus *Neocallichirus* Sakai possess a highly curved tip of the movable finger, but the carpus is narrower proportionally than that of CM 39654. Species of *Callianassa* Leach sensu stricto possess a highly curved movable finger, but the merus has a prominent spine which is not observable in CM 39654 due to the incomplete preservation of the merus. Species of the genus *Neotrypaea* have a very similar movable finger to CM 39654, but the manus of species of *Neotrypaea* is too short compared to the finger and to the carpus to accommodate CM 39654. Species of *Notiax* Manning and Felder have a movable finger, manus, and carpus that could be comparable to the new material, but species of *Notiax* possess a meral spine not observable in CM 39654. Consequently, characters of CM 39654 cannot permit tentative referral of *C.* cf. *C. porterensis* sensu lato to a known genus.

*Callianassa* sensu lato species 1  
(Fig. 3D)

**Diagnosis.**—Callianassid with large, sharp, spinelike tooth on the fixed finger of the manus of the first pereopod.

**Description.**—Manus about twice as long as high ( $H/L = 0.49$ ), rectangular; inner surface smooth, weakly convex, flattening near base of fixed finger; proximal margin nearly straight, upper and lower margins parallel and straight; distal margin nearly straight, longitudinal inflated region paralleling distal margin.

Fixed finger weakly rimmed on lower margin, length of finger 0.32 total manus length, stout proximally and narrowing distally; inner surface with ridge extending from base to approximately two-thirds length of finger, ridge terminating rather abruptly, ridge projecting obliquely downward at about  $120^\circ$  angle from distal margin of manus; tip curving into small hook, finger bearing stout, sharp, triangular tooth about one-third distance from distal margin of manus.

**Measurements.**—All measurements are in millimeters. L (maximum of manus) = 18.2; H (maximum of manus) = 9.0; L (maximum of inner surface of fixed finger) = 5.9.

**Referred Specimens.**—The sole specimen, CM 39660, is deposited in the Carnegie Museum of Natural History.

**Locality and Stratigraphic Position.**—The specimen was collected in a concretion as float from RB36.

**Remarks.**—The specimen consists only of the inner surface of the manus and fixed finger of a cheliped; it is uncertain as to whether the cheliped is major or

minor. The overall rectangular shape of the chela and the relatively short fixed finger indicate that it is more likely that the chela is a major claw rather than a minor one. This specimen is unlike any other previously described callianassid or ctenochelid from the Pacific Northwest, and no known extant genera possess a large, sharp tooth on the fixed finger such as is present in *Callianassa* sensu lato sp. 1. Some extant thalassinoid genera do possess a tooth or spine on the fixed finger, but none can be compared positively with *Callianassa* sensu lato sp. 1. The male of *Callianopsis* possesses a blunt tooth about midway along the fixed finger of the major chela, but the tooth on *Callianassa* sensu lato sp. 1 is positioned nearer the base of the finger and is much sharper and more toothlike. The major chela of the female *Callianopsis* possesses a sharp, triangular tooth at the base of the fixed finger, but the tooth is smaller and is not positioned as far along the fixed finger as the tooth in *Callianassa* sensu lato sp. 1. The minor chela of the male *Callianopsis* possesses a sharp, toothlike projection positioned near the base of the finger, but the hand and fingers of the minor chela of *Callianopsis* are of a different nature than those of *Callianassa* sensu lato sp. 1. The minor chela of *Callianopsis* tends to be more equidimensional and the fixed finger is much longer than the finger on the specimen under study. Specimens referred to the genus *Dawsonius* Manning and Felder possess a tooth on the fixed finger of the major chela, but the tooth is blunt and positioned just distally of the midlength of the finger (Manning and Felder, 1991). Specimens referred to the genus *Paracalliax* de Saint Laurent possesses a blunt tooth on the fixed finger of the minor chela, but the tooth is much smaller and less sharp than that of *Callianassa* sensu lato sp. 1 and the finger is much longer in specimens referred to *Paracalliax* (de Saint Laurent and Le Loeuff, 1979). Confident generic placement of the sole specimen of *Callianassa* sensu lato sp. 1 awaits the discovery of better material because only one specimen with this form was recovered from Pysht deposits, and there are no others like it, as far as is known, from Twin River Group deposits.

Family Ctenochelidae Manning and Felder, 1991

Subfamily Callianopsinae de Saint Laurent, 1973

Genus *Callianopsis* de Saint Laurent, 1973

*Callianopsis clallamensis* (Withers, 1924)

*Callianassa clallamensis* Withers, 1924:122; Rathbun, 1926:114; Berglund and Goedert, 1992:2–3.

*Callianassa twinensis* Rathbun, 1926:115; Berglund and Goedert, 1992:2–3.

*Callianopsis clallamensis* Hopkins and Feldmann, 1997.

*Referred Specimens.*—Several specimens are deposited in the Carnegie Museum of Natural History under the number CM 39691.

*Localities and Stratigraphic Position.*—Specimens referable to this species were collected from RB18, RB19, and RB38. Most specimens were collected from RB18.

*Remarks.*—Hopkins and Feldmann (1997) referred both *Callianassa clallamensis* Withers and *Callianassa twinensis* Rathbun to the genus *Callianopsis* de Saint Laurent and synonymized the two species, with *Callianopsis twinensis* (Rathbun) being the junior synonym. Individuals originally referable to *C. clallamensis* are males while those originally referable to *C. twinensis* are females (Hopkins and Feldmann, 1997). Over 90 specimens referable to this species have been collected from the Pysht Formation, and they are by far the most abundant of any of the decapods of the Pysht Formation.



Infraorder Brachyura Latreille, 1803  
Section Heterotremata Guinot, 1977  
Superfamily Calappoidea de Haan, 1833  
Family Calappidae de Haan, 1833  
Subfamily Calappinae de Haan, 1833  
Genus *Mursia* Desmarest, 1823

*Type Species.*—*Mursia cristiata* H. Milne Edwards, 1837.

*Diagnosis.*—Calappid with transversely ovoid outline, strong lateral spines, and usually with rows of tubercles arranged on longitudinal ridges on the dorsal carapace. Chelae with row of small denticles on upper margin; merus of chelipeds sometimes possessing pronounced spine.

*Description.*—See Rathbun, 1937.

*Remarks.*—In addition to the characters commonly listed as diagnostic of the genus *Mursia*, almost every species possesses rows or ridges of tubercles, usually one medial and two or three on each branchial region. In the absence of rows of tubercles, the entire dorsal carapace surface may be coarsely granular as in *Mursia mcdowellii* Manning and Chace.

All species named on the basis of dorsal carapace morphology, except *Mursia obscura* Rathbun, possess lateral spines. Because of the absence of lateral spines and its narrow carapace, *M. obscura* was reassigned to *Paramursia* Karasawa by Karasawa (1991:14). The length of the lateral spines varies among authentic species of the genus *Mursia*, ranging from about half the total carapace width in *Mursia marcusana* Rathbun, to short denticles such as those of *Mursia microspina* Davie and Short. Lateral spine length may also vary among individuals within a species. For example, *Mursia armata* de Haan may possess lateral spines half as long as the total carapace width (Sakai, 1976); however, some specimens examined in the United States National Museum of Natural History (USNM 63715) possessed much shorter lateral spines.

Rathbun (1937:215) described the meri of the major chelipeds of *Mursia* as possessing a "distal ridge with one or more spines." The length of these meral spines appears to be highly variable within the genus. They are much reduced in *M. hawaiiensis* Rathbun, *M. microspina*, *M. flamma* Galil, *M. danigo* Galil, *M. aspera* Alcock, and *M. armata*. In *M. africana* Galil, *M. musorstomia* Galil, *M. australiensis* Campbell, *M. curtispina* Miers, and *M. trispinosa* Parisi, they are intermediate in size. *Mursia spinimanus* Rathbun displays a prominent meral spine. There may be a weak correlation between lateral spine length and meral spine length, with those species possessing long lateral spines having somewhat longer meral spines.

Several genera are similar in dorsal carapace morphology to *Mursia*. The genus *Cycloes* de Haan possesses an overall narrower carapace than *Mursia* and shorter lateral spines than *Mursia*. In *Cycloes*, the lateral spines are directed posterolaterally while in *Mursia* those spines are directed laterally. Members of the genus *Cycloes* lack coarse carapace ornamentation which distinguishes them from species of *Mursia*. The genus *Paramursia* Karasawa was erected for fossil specimens possessing a round carapace with very short lateral spines which cannot be accommodated in *Mursia* (Karasawa, 1989). The genus *Acanthocarpus* Stimpson possesses a nearly equidimensional, ovate carapace while *Mursia* is transversely ovoid. In *Acanthocarpus*, the anterolateral and posterolateral margins are contin-

uous while in members of the genus *Mursia*, the carapace possesses a convexly rounded anterolateral margin and a straighter, constricted, narrowing posterolateral margin. *Acanthocarpus* lacks strong ridges of tubercles on the dorsal carapace, which is characteristic of *Mursia*. Finally, the strong spine of *Acanthocarpus* is placed on the posterolateral margin and is directed posterolaterally while in *Mursia* the spine is positioned and directed laterally from the carapace. The genus *Platymera* H. Milne Edwards differs from *Mursia* in several aspects of the carapace and appendages, including possession of fine granules on the carapace instead of coarse granules as in *Mursia* (Galil, 1993:373). The genus *Platymera* had been synonymized with *Mursia* by many authors but was reinstated by Galil (1993).

The specimens described herein exhibit a suite of characters diagnostic of species of the genus *Mursia* including ridges with rows of tubercles; well-developed, lateral spines directed laterally; and a transversely ovoid carapace. They also possess a strong meral spine on the chelipeds, which has not been noted as characteristic of the genus *Mursia*. Therefore, the specimens herein described may be placed in the genus *Mursia*, and the diagnosis for the genus is therefore broadened to accommodate the strong meral spines of the specimens.

*Mursia marcusana* Rathbun, 1926

(Fig. 4, 5)

*Mursia marcusana* Rathbun, 1926:82; Feldmann et al., 1991:356.

**Diagnosis.**—Calappid with transversely ovoid outline, extremely long lateral spines, sinuous posterolateral margins, and five strong dorsal carapace ridges ornamented with tubercles in addition to two rows of tubercles not placed on ridges. Major cheliped with pronounced meral spine.

**Emendation to Description.**—Carapace transversely ovoid; vaulted longitudinally and laterally; maximum carapace width at position of long lateral spine at midlength, spines occupying about 55% maximum carapace width including spines; front narrow (frontal width/maximum carapace width without lateral spines = 0.10), downturned, sulcate, finely granular, projecting short distance beyond orbits; orbits large, subelliptical, closely spaced, rimmed on upper surface, bearing short fissure centrally on upper margin, bearing subtle outer orbital projection, orbital rim protruding slightly at inner orbital corner, fronto-orbital margin occupying 55% maximum carapace width excluding lateral spines; anterolateral margin convex, rounded, bearing rim of small rounded denticles; posterolateral margin somewhat sinuous and slightly concave; posterior margin narrow, approximately 20% maximum carapace width excluding lateral spines, bearing small blunt tooth on each corner.

Carapace ornamented with tubercles and tuberculate ridges; mesogastric, urogastric, and cardiac regions situated on medial ridge; mesogastric region narrow anteriorly and widening posteriorly, pair of small tubercles near middle, one large tubercle near posterior margin; urogastric region narrow, as wide as mesogastric region; cardiac region long, sinuous lateral margins, bearing three axial tubercles with posteriormost being smallest; all three medial regions inflated, bounded by distinct grooves.

Protogastric region bearing numerous small tubercles, delimited by shallow cervical groove on distal margin but demarcation between mesogastric region and protogastric region indistinct. Cervical groove curving convexly from anterolateral margin, outlining lateral and posterior margin of mesogastric region. Branchial region bearing row of three tubercles not situated on ridge, row closely paralleling anterolateral margin, most distal tubercle in row smallest, situated close to middle tubercle of row; branchial region bearing two major ridges with tubercles; first ridge paralleling anterolateral margin, extending from base of protogastric region, terminating at base of lateral spine, bearing about five tubercles; second extending obliquely from posterolateral margin to protogastric region, bearing about five tubercles of unequal size; ridge bifurcating about midway along second ridge, short bifurcating ridge extending obliquely towards front and bearing about two tubercles. Rounded tubercle present on either side of urogastric region; row of tiny tubercles paralleling groove outlining urogastric region and proximal portion of cardiac region; surfaces of the carapace between ridges finely granular.

Sternites finely granular; sternite 1 unknown; sternites 2, 3, and 4 fused; sternite 3 narrow with



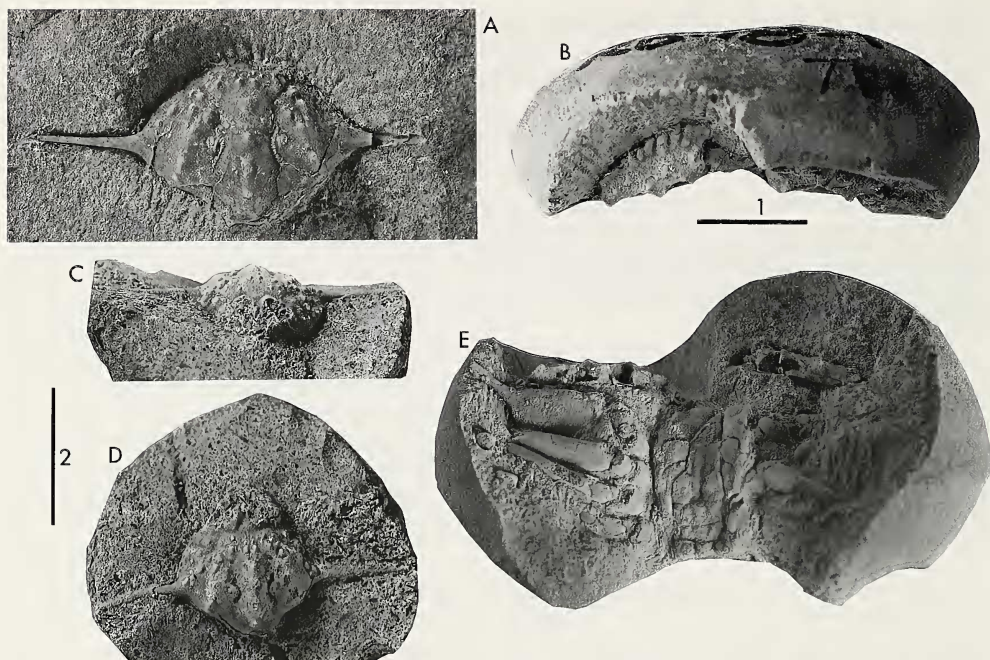


Fig. 4.—*Mursia marcusana* Rathbun. A. Dorsal view of nearly complete carapace, CM 39663. B. Lateral view of outer surface of major chela, CM 39665. C. Anterior view of nearly complete carapace, CM 39665. D. Dorsal view, CM 39661. E. Ventral view showing meral spine at upper left, CM 39665. Scale bar 1 for A, B, and E. Scale bar 2 for C and D. Scale bars = 1 cm.

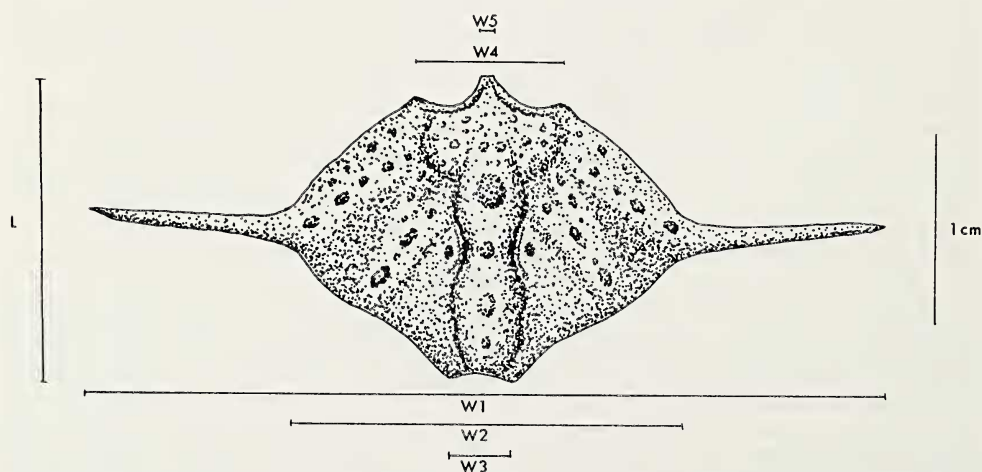


Fig. 5.—Reconstruction of *Mursia marcusana* Rathbun showing the position and orientation of measurements made.



small distal hook, directed anterolaterally; sternite 4 narrow, directed anterolaterally, long narrow distal hook; sternite 5 longest, directed laterally, distal hook long and narrow; sternite 6 directed posterolaterally, narrow, very long, stout distal hook; sternites 7 and 8 unknown. Abdomen slightly more than half as wide as sternum; telson isosceles triangular in shape; sixth somite as long as broad, slightly wider than telson and slightly shorter; fifth somite about two-thirds as long as sixth but about half again as wide; somites 1–4 becoming progressively shorter but maintaining same width.

Coxae of pereopods 1–4 cylindrical, about as long as wide, about same size; ischia and bases of pereopods 2–4 fused, slightly longer than wide; meri of pereopods 2 and 3 much longer than wide, appearing to be flattened oval in cross section, margins not well known.

Carpus of major cheliped unknown; merus of major cheliped longer than high, margin articulating with ischium sinuous, bearing long spine on margin articulating with carpus, spine broken but appearing to be at least half as long as merus measured without meral spine. Major and minor chelae subequal, wide distally and narrowing proximally, bearing tuberculate crest on upper margin, lower margin with three to four small spines; outer surface of manus ornamented with numerous tubercles; fixed finger not known; movable finger short, stout, lower margin ornamented with three or four stout tubercles.

**Measurements.**—All measurements are in millimeters. CM 39663, W1 (maximum, including lateral spines) = 42.6, W2 (maximum, excluding lateral spines) = 19.4, W3 (posterior) = 3.6, L (maximum) = 15.8. CM 39661, W1 (maximum, including lateral spines) = 23.1, W2 (maximum, excluding lateral spines) = 10.0, W3 (posterior) = 2.6, W4 (fronto-orbital) = 5.5, W5 (frontal) = 1.0, L (maximum) = 9.8. CM 39665, W (maximum of sternum) = 9.3, W (maximum width of sixth somite) = 3.6, L (maximum of sixth somite) = 3.6, W (maximum of fifth somite) = 5.1, L (maximum of fifth somite) = 2.4, L (maximum of abdomen) = 14.0, L (maximum of telson) = 3.9, W (maximum of telson) = 3.0. Merus of third pereopod, L = 9.0. Merus of fourth pereopod, L = 8.6. Major cheliped, L (merus) = 8.5, L (meral spine) > 4.3, L (maximum of manus) = 13.4, L (dactylus) = 5.1. Minor cheliped, L (maximum of manus) > 11.3. CM 39662, W (maximum excluding lateral spines) = 21.8 (based on half measures), L (maximum) > 15.8. Position and orientation of dorsal carapace measurements illustrated in Figure 5.

**Referred Specimens.**—Six specimens referred to this species, CM 39661–39666, are deposited in the Carnegie Museum of Natural History.

**Localities and Stratigraphic Position.**—CM 39662 was collected at site RB37 in thin-bedded siltstone. CM 39663 and CM 39664 were collected as float in concretions at RB38, and CM 39661 was collected as float in a concretion from RB36. CM 39665 and 39666 were collected as float in concretions from RB18.

**Remarks.**—Specimen CM 39663 possesses a dorsal carapace that is preserved mainly as a mold of the interior. The counterpart of this specimen retains some of the integument. Specimen CM 39661 consists of a dorsal carapace only and has remarkably well-preserved orbits and lateral spines. CM 39662 is a flattened dorsal carapace collected in a block of thin-bedded siltstone associated with large quantities of organic matter including molluscs, other decapods, and plant material. CM 39665 possesses a well-preserved venter including part of the abdomen and sternum, chelipeds, and other pereopods. CM 39666 possesses part of the abdomen and sternum only, and CM 39664 possesses a fragment of the dorsal carapace.

The specimens are referable to *Mursia marcusana* for several reasons. Although the specimen described by Rathbun (1926) is broken, ridges and arrangement of dorsal carapace tubercles can be observed, and the new material closely resembles the type material in these respects. Also, Rathbun (1926) reported that her specimens possessed a “strong lateral spine broken off at the base” (p. 82)

as well as five well-developed ridges with strong tubercles, all of which the specimens referred to *M. marcusana* possess. The discovery of the material under study, preserving intact lateral spines, complete dorsal carapaces, a well-preserved venter, and chelae allows for a much more complete description of the species.

Specimens possessing only the ventral aspect are confidently referred to *Mursia marcusana* for several reasons. The venter and the chelipeds are typical of mursiids, both recent and fossil. *Mursia marcusana* is the only calappid and only mursiid recovered as yet from the Pysht Formation, and it seems unlikely that the venters would belong to a previously undescribed calappid from the Pysht Formation. Finally, the presence of extremely long lateral spines on the carapace and pronounced meral spines in the same animal is likely since the spines could be adapted for similar or identical functions.

In respect to the long meral spines, the specimens resemble species of the genus *Acanthocarpus*, which possess very pronounced meral spines. However, the material here assigned to *Mursia marcusana* differs from species of *Acanthocarpus* in several important aspects as has been discussed. Because the specimen possessing the venter and chelae is referable to *M. marcusana*, the diagnosis for the genus *Mursia* must be broadened to accommodate the long meral spines.

This material from the Pysht Formation extends the geographic range of *Mursia marcusana* as reported by Rathbun (1926). She reported specimens from Bainbridge Island, Washington, from the upper Oligocene Blakely Formation and from Alki Point on Puget Sound, near Seattle, in upper Oligocene rocks. Feldmann et al. (1991) figured this species from the Pysht Formation of Washington but did not discuss it. Other species of *Mursia* have previously been reported from Oligocene rocks, including *M. yaquinensis* Rathbun of Oregon and *M. mcdonaldi* Rathbun of Panama.

*Mursia marcusana* can be distinguished from all other species of *Mursia* because of its extremely long lateral spines, long meral spines, and unique arrangement of tubercles on strong ridges. The species most similar to *M. marcusana* are *M. takahashii* Imaizumi from the Pliocene of Japan and *M. minuta* Karasawa from the Miocene of Japan. *Mursia takahashii* has shorter lateral spines and less pronounced tubercle-bearing ridges than *Mursia marcusana*. The arrangement of tubercles on *M. takahashii* is different because the most axially placed branchial ridge of tubercles of *M. takahashii* does not appear to bifurcate as seen in *M. marcusana*. The posterolateral margins of *M. takahashii* are relatively straight while those of *M. marcusana* are sinuous. Finally, the posterolateral margins of *M. marcusana* are much more constricted than those of *M. takahashii*.

*Mursia marcusana* can be distinguished from *M. minuta* Karasawa because *M. minuta* has a much more convex anterolateral margin, and the arrangement of carapace ridges is somewhat different in *M. minuta* because it does not possess a bifurcating ridge. The cardiac region of *M. minuta* possesses only two axial tubercles while *M. marcusana* possesses three on that region.

Among extant mursiids, *Mursia armata* most closely resembles *M. marcusana*. Both species possess long lateral spines, a convexly rounded anterolateral margin, highly constricted posterolateral margins, and short posterior margins with small denticles on each corner. The two species differ in several important ways, however. *Mursia armata* possesses seven ridges with tubercles while *M. marcusana* possesses five ridges of tubercles and two rows of tubercles not positioned on ridges. *Mursia armata* also lacks the numerous small tubercles on the protogastric



Table 3.—Known species of *Mursia*, collecting locale, age, and depth at which specimens were collected.

Taxon	Locality	Age	Depth (m)
<i>M. africana</i> Galil	East Africa	Recent	250–290
<i>M. australiensis</i> Campbell	West Pacific	Recent	40–320
<i>M. danigoi</i> Galil	Phillipines	Recent	143–204
<i>M. flamma</i> Galil	South Africa	Recent	35–510
<i>M. musorstomia</i> Galil	New Caledonia	Recent	420–575
<i>M. cristimanus</i> de Haan	South Atlantic	Recent	unknown
<i>M. cristata</i> H. Milne Edwards	Indian Ocean	Recent	70–318
<i>M. armata</i> de Haan	Japan	Recent	50–150
<i>M. spinimanus</i> , Rathbun	Hawaii	Recent	95–435
<i>M. bicristimana</i> Alcock and Anderson	Indian Ocean	Recent	217–397
<i>M. curtispina</i> Miers	Japan	Recent	30–150
<i>M. mcdowelli</i> Manning and Chace	Ascension Island	Recent	122–152
<i>M. hawaiiensis</i> Rathbun	Hawaii	Recent	97–730
<i>M. trispinosa</i> Parisi	Japan	Recent	65–120
<i>M. aspera</i> Alcock	Japan	Recent	65–150
<i>M. microspina</i> Davie and Short	Australia	Recent	210
<i>M. minuta</i> Karasawa	Japan	early Pliocene	—
<i>M. lienharti</i> (Bachmayer)	Central Europe	Miocene	—
<i>M. takahashii</i> Imaizumi	Japan	Miocene	—
<i>Mursia</i> sp. Karasawa	Japan	mid-Miocene	—
<i>Mursia</i> sp. Förster	Poland	mid-Miocene	—
<i>M. mcdonaldi</i> Rathbun	Panama	Oligocene	—
<i>M. yaquinesis</i> Rathbun	Northwest United States	Oligocene	—
<i>M. marcusana</i> Rathbun	Northwest United States	Oligocene	—

region seen in *M. marcusana*, and the lateral spine of *M. armata* is shorter and more stout. Finally, *M. armata* lacks the strong meral spine seen in *M. marcusana*.

Species referred to *Mursia* are widely distributed geographically and inhabit a wide range of depths (Table 3). For example, *M. armata* has been reported from depths of 25–150 m, while *M. hawaiiensis* has been reported from 97–730 m in waters off Japan (Rathbun, 1893). Five species from Japan were collected from soft muddy or sandy bottoms at outer sublittoral depths (Sakai, 1976). *Mursia takahashii* was reported by Imaizumi (1952) to have been collected from the lower to middle Miocene Natori Group, which is characterized by fossils representing a warm-water fauna. Karasawa (1993) listed the Japanese *Carcinoplax prisca*–*M. minuta* assemblage as having inhabited a subtropical climate of the late Miocene and early Pliocene. Recent species are distributed from tropical to temperate climates, and those that are found in tropical climates inhabit deeper waters than those found in more temperate climates.

Superfamily Corystoidea Samouelle, 1819

Family Atelecyclidae Ortmann, 1893

Genus *Trichopeltarion* A. Milne Edwards, 1880

*Type Species.*—*Trichopeltarion nobile* A. Milne Edwards, 1880.

*Remarks.*—Many authors have discussed the fact that *Trichopeltarion* A. Milne Edwards and *Trachycarcinus* Faxon are closely related, if not indistinguishable from one another. The three most obvious similarities are the possession of numerous marginal spines, a tridentate rostrum, and a carapace ornamented with



numerous tubercles. Most keys to the two genera fail to satisfactorily distinguish the two genera. For example, in his key to the Atelecyclidae, Sakai (1976) characterized *Trichopeltarion* as possessing an oval outline, tuberculate dorsal carapace, tridentate front, and toothed lateral margins (p. 311). *Trachycarcinus* was characterized as having the same characters except with a subpentagonal outline (Sakai, 1976:311), and many authors have argued that this similarity in characteristics makes the distinction between the two genera rather arbitrary (Dell, 1969; Guinot, 1986, 1989). Alcock and Anderson (1899) remarked that the separation of the two was "doubtful" (p. 10). Rathbun (1930) expressed doubt on the validity of the two genera by stating, "If the three genera *Peltarion*, *Trichopeltarion*, and *Trachycarcinus* be retained. . ." (p. 165). She described *Trichopeltarion* as possessing a subcircular carapace, spinose borders, and a tridentate front, among several other characters (Rathbun, 1930:168). She characterized *Trachycarcinus* as having a pentagonal carapace, toothed anterolateral margins, and a tridentate front, among several other characters (p. 164). Dell (1969) wrote that he, "preferred to unite *Trachycarcinus* with *Trichopeltarion*," because he believed that differences in tuberculation of the dorsal carapace were "differences of degree" and also that the use of length of the lateral spines to distinguish the two genera was arbitrary (p. 370). Guinot (1986, 1989) noted these concerns but did not offer a satisfactory solution to the problem of distinguishing the two genera. Although the specimens described herein conform well to the diagnosis for the genus *Trachycarcinus*, the overall difficulty associated with distinguishing *Trichopeltarion* and *Trachycarcinus* prompts us to follow Dell's (1969) suggestion to synonymize the two genera and to refer the new specimens to *Trichopeltarion*. All species that have been previously referred to *Trachycarcinus* are hereafter referred to the genus *Trichopeltarion*. A systematic revision of the genus *Trichopeltarion* and the family Atelecyclidae which will address the *Trichopeltarion*-*Trachycarcinus* problem in detail is in progress (Salva, personal communication).

*Trichopeltarion berglundorum*, new species

(Fig. 6, 7)

*Trachycarcinus* sp. Feldmann et al., 1991:356; Berglund and Goedert, 1992:3.

**Diagnosis.**—Atelecyclid with 15 simple carapace spines, oval to subpentagonal outline, well-developed carapace regions, and large granular tubercles.

**Description.**—Carapace oval to subpentagonal, slightly longer than wide, moderately vaulted both transversely and longitudinally, rather coarsely punctate in advance of cervical groove, finely punctate posteriorly; tumid carapace regions moderately well defined by grooves; carapace margin bearing 15 narrow triangular spines.

Fronto-orbital margin measured from tips of postorbital spines about 62% total carapace width measured between tips of posteriormost set of spines; anterolateral margin convex, long. Front moderately produced beyond orbits, bearing three spines, central spine stoutest. Orbits bounded by pre- and postorbital spines with intercalated spine; pre-orbital spine triangular, directed forward; intercalated spine narrow, sharp, directed anterolaterally; postorbital spine longest, directed anterolaterally. Anterolateral margin with three spines not including postorbital spine, first and third longest, narrow; second smaller, broadly triangular; all three directed laterally. Posterolateral margin convex; posterior margin not well known but appearing to be narrow.

Grooves moderately deep; cervical groove curving slightly posteriorly from just behind first anterolateral spine, continuing across carapace to medial region, then abruptly curving posteriorly, crossing medial region between mesogastric and urogastric regions; weak groove separating protogastric and hepatic region extends from between intercalated and postorbital spine to cervical groove; axial regions bounded by deep grooves.

Frontal region flattened with central shallow sulcus terminating at base of central rostral spine;

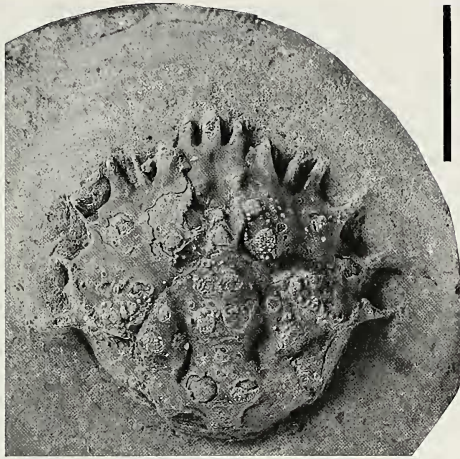


Fig. 6.—*Trichopeltarion berglundorum*. Dorsal view of holotype, CM 39667. Scale bar = 1 cm.

mesogastric region triangular, slightly granular, large tubercle situated anteriorly, granular bilobed swelling posteriorly; protogastric region granular, small, smooth tubercle near front on either side of medial sulcus, two large granular tubercles along axial margin; hepatic region small, triangular, granular, bearing one large granular tubercle; branchial region large, not subdivided, bearing numerous granules and four large granular tubercles, region elevated anteriorly, elevated region bearing large granular tubercles; urogastric region narrow, bearing pair of large granular tubercles; cardiac region pentagonal in shape, apex of pentagon directed posteriorly, bearing four granular tubercles arranged in diamond pattern with middle two tubercles largest; intestinal region obscure.

Venter and appendages unknown.

**Measurements.**—All measurements are in millimeters. CM 39667, carapace,

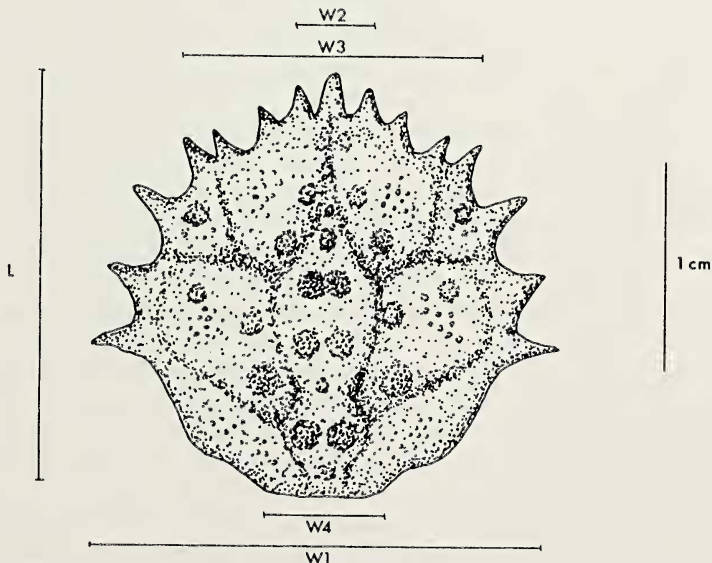


Fig. 7.—Reconstruction of *Trichopeltarion berglundorum* showing the position and orientation of measurements made.

W1 (maximum) = 22.1, L (maximum) = 21.0, W2 (frontal) = 7.0, W3 (fronto-orbital) = 13.8, W4 (posterior) = 5.8. CM 39668, carapace, W1 (maximum) > 13.9, L (maximum) = 15.1. Position and orientation of dorsal carapace measurements illustrated in Figure 7.

*Types*.—The holotype, CM 39667, and a paratype, CM 39668, are deposited in the Carnegie Museum of Natural History.

*Localities and Stratigraphic Position*.—CM 39667 was collected in a concretion as float at RB18 and CM 39668 was collected in a concretion as float at RB15.

*Etymology*.—The trivial name honors Ross and Marion Berglund of Bainbridge Island, Washington, who donated much of the material forming the basis of this study and whose contributions to the study of Tertiary decapods from the Pacific Northwest have been invaluable.

*Remarks*.—The two specimens referred to this new species were preserved in concretions. Both retain original carapace material with CM 39667 exhibiting a complete carapace and CM 39668 a broken carapace. The counterparts for each are not known.

*Trichopeltarion berglundorum* differs from *T. nobile*, *T. fantasticum* Richardson and Dell, *T. wardi* Dell, and *T. greggi* Dell in its possession of simple, small marginal spines as opposed to the complex spines of all of these species. The new species most closely resembles *T. huziokai* Imaizumi from the Miocene of Japan. Both species possess a rounded to subpentagonal carapace outline, similar spine shape and arrangement, and a similar arrangement of carapace regions. However, *T. huziokai* bears numerous prominent tubercles on the carapace while *T. berglundorum* bears small tubercles on some regions. *Trichopeltarion berglundorum* bears large granular tubercles on several regions which are absent in *T. huziokai*. *Trichopeltarion huziokai* Imaizumi bears numerous tubercles on the branchial region while *T. berglundorum* bears few if any on that region. The medial regions on *T. huziokai* are better differentiated than on *T. berglundorum*. *Trichopeltarion berglundorum* possesses better developed carapace spines, a less rounded carapace, and less inflated regions than does *T. inflatus* Kato. *Trichopeltarion berglundorum* differs from *T. decorus* Rathbun from the Miocene of Panama in several respects. *Trichopeltarion decorus* possesses very small carapace tubercles, carapace margins with numerous small spines, and slightly tumid carapace regions delimited by shallow grooves, while *T. berglundorum* has large granular carapace tubercles, large carapace spines, and tumid carapace regions.

*Trichopeltarion berglundorum* differs from nearly all recent species of *Trichopeltarion* in having a rounded to subpentagonal carapace instead of a pentagonal one. Many recent species including *T. foresti* Guinot, *T. glaucus* Alcock and Anderson, *T. balssi* Rathbun, *T. alcocki* Doflein, *T. crosnieri* Guinot, *T. sagmaiensis* Rathbun, and *T. spinulifer* Rathbun, bear numerous intercalated spines between the larger anterolateral spines and some have spines which are themselves armed with small denticles; *Trichopeltarion berglundorum* exhibits neither condition. Several recent species have more ornamented carapaces and a more produced front than *T. berglundorum* including *T. foresti*, *T. glaucus*, *T. delli* Guinot, *T. crosnieri*, and *T. corallinus*. *Trichopeltarion berglundorum* is similar to many recent species of *Trichopeltarion* in possessing simple carapace spines and in the arrangement of large granular carapace tubercles, including *T. moosai* Guinot, *T. corallinus*, *T. hystricosus* Garth, *T. elegans* Guinot and Sakai, *T. delli*, and *T. intesi* Crosnier. *Trichopeltarion berglundorum* can be distinguished from *T. delli*



Table 4.—All known species of *Trichopeltarion* and the collecting locale, age, and depth at which specimens were collected.

Taxon	Geographic range	Age	Depth (m)
<i>T. nobile</i> Milne Edwards	Caribbean	Recent	150–400
<i>T. fantasticum</i> Dell and Richardson	New Zealand	Recent	180–730
<i>T. wardi</i> Dell	Southwest Pacific	Recent	80–140
<i>T. hystricosus</i> Garth	Southeast Pacific	Recent	200–1124
<i>T. corallinus</i> Faxon	Southeast Pacific	Recent	834–1280
<i>T. crosnieri</i> Guinot	Madagascar	Recent	480–700
<i>T. spinulifer</i> Rathbun	Gulf of Mexico	Recent	324–347
<i>T. alcocki</i> Doflein	Indo-Pacific	Recent	750–1650
<i>T. ovalis</i> (Anderson)	Indo-Pacific	Recent	100–397
<i>T. moosai</i> Guinot	Indo-Pacific	Recent	313
<i>T. foresti</i> Guinot	Indo-Pacific	Recent	395–450
<i>T. delli</i> Guinot	Indo-Pacific	Recent	425–595
<i>T. balssi</i> Rathbun	Japan	Recent	50–200
<i>T. sagamiensis</i> Rathbun	Japan	Recent	85–200
<i>T. elegans</i> Guinot and Sakai	Japan	Recent	100–150
<i>T. intesi</i> Crosnier	Ivory Coast	Recent	600
<i>T. glaucus</i> Alcock and Anderson	Indian Ocean	Recent	780
<i>T. huziokai</i> Imaizumi	Japan	Miocene	—
<i>T. decorus</i> Rathbun	Fiji	Miocene	—
<i>Trachycarcinus berglundorum</i> n. sp.	Northwest Washington USA	late Olig.– early Miocene	—
<i>T. inflatus</i> Kato	Japan	Miocene	—
<i>T. greggi</i> Dell	New Zealand	late Miocene	—

and *T. moosai* because it has a more oval outline and shorter spines. *Trichopeltarion berglundorum* does not possess fine perliform granules over the entire carapace as does *T. intesi*. *Trichopeltarion berglundorum* has a more circular carapace than does *T. hystricosus* and the spines of *T. berglundorum* are much less developed and produced than those of *T. hystricosus*. *Trichopeltarion elegans* has longer and more produced spines than does *T. berglundorum*. *Trichopeltarion corallinus* is much more distinctly pentagonal in shape than *T. berglundorum* and has somewhat different axial ornamentation than does *T. berglundorum*.

*Trichopeltarion berglundorum*, collected from the upper Oligocene to lower Miocene deposits of the Pysht Formation, represents one of the earliest known species of *Trichopeltarion*, suggesting a possible north Pacific origin. Several other fossil species are Miocene in age and include material from Fiji and Japan. *Trichopeltarion greggi* is known from the middle–late Miocene of New Zealand (Dell, 1969; Feldmann and Keyes, 1992). Recent species are known from the Caribbean Sea, the Gulf of Mexico, the Indo-Pacific and New Zealand (Table 4).

Most recent species of *Trichopeltarion* are found in very deep water (Table 4). Garth and Haig (1971) reported that specimens of *T. hystricosus* have several adaptations to deep water including eye size and pigmentation. A female specimen of *T. hystricosus* carried a small clutch of large eggs, while related species inhabiting shallower depths would be expected to have larger clutches of smaller eggs (Garth and Haig, 1971). Alcock and Anderson (1899) also reported that dredged females of the species *T. glaucus* carried a small number of large eggs. Garth and Haig (1971) speculated that this was an adaptation to deep water in which the larval stage would be abbreviated and there would be little exposure to pelagic dispersal. Recent species range widely in comparable depths (Table 4).

Karasawa (1993) inferred from the depths of recent species of *Trichopeltarion* found in Japan that *T. huziokai* must have inhabited the outer sublittoral to upper bathyal zones. His assertion was corroborated by the fact that living forms of *Carcinoplax* also inhabit deep waters, and a fossil species of *Carcinoplax* was found associated with specimens of *T. huziokai*. *Trichopeltarion glaucus* was reported by Alcock and Anderson (1899) in association with living and dead corals.

Superfamily Portunoidea Rafinesque, 1815  
Family Portunidae Rafinesque, 1815  
Subfamily Carcininae Macleay, 1838  
Genus *Portunites* Bell, 1858

*Type Species.*—*Portunites incerta* Bell, 1858.

*Remarks.*—The specimens described here are conspecific with material Rathbun (1926) named *Portunites triangulum*. This species is retained in the genus *Portunites* at this time based on several criteria. According to Glaessner (1969), *Portunites* is defined as possessing a carapace that is not much broader than long, a front with four teeth, an anterolateral margin with three or four teeth excluding the outer-orbital spine, a posterolateral margin that is straight or slightly concave, well-marked gastrodurocardiac regions, an arcuate ridge extending from lateral tooth to medial area, and fifth pereopods that are not flattened (p. R513). The specimens described in this study definitely possess all but one of these characters; the fifth pereopods are unknown. The type species of *Portunites*, *Portunites incerta*, exhibits all of the characters noted by Glaessner, except that no fifth pereopod was described for it. The only known species of *Portunites* to have been recovered with an intact fifth pereopod, *P. alaskensis* Rathbun, has a paddlelike fifth pereopod (Tucker and Feldmann, 1990) which contradicts Glaessner's (1969) diagnosis for the genus.

In addition to these criteria, the type species and *Portunites stintoni* Quayle, which was named based upon several paratypes of *P. incerta*, share several other characters. They possess a fronto-orbital margin that occupies two-thirds of the maximum carapace width and orbits with two fissures. Each possesses a longitudinal ridge on the branchial region extending from the posterior margin about three-quarters of the distance on the branchial region. Both species have a similar arrangement of anterolateral spines. The outer orbital spine is stout and directed forward and is similar in size to the third anterolateral spine. The second and fourth anterolateral spines are smaller than the first and third. The fifth anterolateral spine is the longest. The carapace shape of both *P. incerta* and *P. stintoni* is hexagonal. The cardiac regions of both species, especially *P. incerta*, are well defined, and, in *P. incerta* the cardiac region was reported to extend almost to the posterior margin. *Portunites incerta* possesses large stout chelipeds that are unequal in size (Quayle, 1984).

Specimens of *Portunites triangulum* differ from *P. incerta* and *P. stintoni* in several of these characters. They possess a weak longitudinal branchial ridge that terminates in a strong tubercle; the ridge is not nearly as obvious as those on *P. incerta* or *P. stintoni*. *Portunites triangulum* possesses an anterolateral margin whose length is equal to one-half the maximum width of the carapace, not two-thirds of the width of the carapace. *Portunites triangulum* is almost half again as wide as long, while *P. incerta* and *P. stintoni* are less wide. The anterolateral



teeth of *P. triangulum* become gradually larger laterally, with the fifth being the largest; this is different than the condition observed in either *P. incerta* or *P. stintoni*. The regions of *P. triangulum* are not as well defined, the overall carapace shape is less squarely hexagonal, and the chelipeds are narrower and longer than those of *P. incerta* or *P. stintoni*. However, these differences do not appear to be generic at this time and may constitute specific differences among species of *Portunites*. *Portunites triangulum* possesses all of the diagnostic characters for species of the genus and is therefore retained in it.

However, analysis of published plates of the Japanese fossil genera *Itoigawaia* and *Minohellenus* suggests that *P. triangulum* may be better accommodated in one of those two genera. Confirmation awaits examination of type material housed in Japan. Karasawa et al. (1992) erected the genus *Itoigawaia* for fossil material differing from *Portunites* in lacking a ridge separating the cephalic and branchial regions of the carapace. The type species of *Itoigawaia*, *I. minoensis*, was originally assigned to the genus *Portunites* and was later removed because of the lack of a transverse ridge (Karasawa et al., 1992). Examination of published plates of *Itoigawaia* shows that some specimens appear to have a very weakly developed ridge in the same position as that seen in species of *Portunites* (Karasawa et al., 1992; Karasawa, 1993). *Itoigawaia* possesses a length-to-width ratio, frontal margin, and carapace region configuration that could easily accommodate another taxon endemic to Japan, *Minohellenus*, which is superficially similar to *Portunites* and is quite similar to the genus *Itoigawaia*. The two genera, *Minohellenus* and *Itoigawaia*, possess similar carapace regions; a very weak transverse ridge separating the cephalic and branchial regions; similar frontal, orbitofrontal, and anterolateral margins; and similar carapace size ratios. Both have chelae that appear to be fairly smooth with keels reported but not observable on the published plates of species of the two genera (Karasawa, 1990; Karasawa et al., 1992; Karasawa, 1993; Kato and Karasawa, 1994, 1996). The fifth lateral spine in *Itoigawaia* is the smallest, while in *Minohellenus*, the fifth anterolateral tooth is largest; this appears to be the only major difference between the two genera, and it is possible that they may be synonymous. The carapace of *Minohellenus* is more transversely ovoid than that of *P. triangulum* and the anterolateral margin is longer relative to the total length (*M. macrocheilus* = 0.62) than in *P. triangulum* (0.55–0.56). The abdomen of species of *Minohellenus* is strongly similar to that of *P. triangulum*; however, this may be a characteristic of the subfamily. *Portunites triangulum* is not referred to either genus at this time because it possesses fairly strong transverse ridges, chelae with a strong lateral keel, and strong tuberculate ornamentation on the branchial regions in the form of a triangle, none of which is possessed by species of either *Minohellenus* or *Itoigawaia* as far as can be discerned from published plates.

The sole species of the monospecific genus *Imaizumilia* Karasawa, *Imaizumilia sexdentata* Karasawa, shares many similarities with species of *Portunites* including the presence of a ridge separating the cephalic and branchial regions and the arrangement of carapace regions and anterolateral spines. It differs from *Portunites* in possessing a wider carapace and a thin orbital margin (Karasawa, 1993). The genus *Imaizumilia* possesses six frontal teeth, including the inner orbital teeth (Karasawa, 1993). This same arrangement occurs in many species of *Portunites*, except in *Imaizumilia* the six teeth appear to be evenly spaced and well defined, while in species of *Portunites* the inner orbital teeth are smaller and closely



spaced. Additionally, carapace regions in *Imaizumila* are much more clearly defined and inflated than those of most species of *Portunites*.

Other portunid genera possess characters similar to those of *Portunites* but are not easily confused with it. The monotypic genus *Pleolobites* was erected by Remy (1960) for specimens collected from Ivory Coast. *Pleolobites* can be immediately distinguished from *Portunites* because *Pleolobites* does not possess the transverse ridge separating the cephalic and branchial regions characteristic of *Portunites*. The genus *Pleolobites* is wider overall than *Portunites*, and the anterolateral spines appear to be more produced at the base and of an overall different shape than those of *Portunites*. Glaessner (1969) pointed out that *Pleolobites* resembles *Xanthilites*. However, examination of the type material would be necessary to confirm the reassignment *Pleolobites erinaceus* Remy.

The genus *Rhachiosoma* bears some resemblance to *Portunites*, but the two differ in several important aspects. *Rhachiosoma* has a more produced lateral spine that is situated posterior to the midpoint of the carapace; in *Portunites*, the spine is somewhat shorter and lies anterior to the midpoint of the carapace. Carapace regions on *Portunites* are somewhat better defined than on *Rhachiosoma*, and *Portunites* bears a ridge that separates the cephalic region from the branchial region; *Rhachiosoma* does not (Feldmann and Maxwell, 1990). One species of *Rhachiosoma* was originally assigned to *Portunites*, *Portunites granulifer* Glaessner. At that time, Glaessner (1960) felt that its closest relative might be *P. triangulum* but later removed it to the genus *Rhachiosoma*; Feldmann and Maxwell (1990) concurred and clarified the numerous differences between *R. granuliferum* and *P. triangulum*.

The species *Cancer araucana* Philippi was removed to *Portunites* by Glaessner (1960:33). Subsequently, Quayle (1984) reported that the species had too many characters that "fall beyond the characters shared by other described species of *Portunites* and it is doubtful if the species should be included in the genus" (p. 176). He based this conclusion on "*Portunites*" *araucana* having six instead of four frontal lobes, longer outer orbital spines, thin inner orbital spines, and an anterolateral margin with five spines, with the fourth and fifth equal in length. A specimen of "*Portunites*" *araucana* was examined by the authors at the United States National Museum of Natural History (USNM 496556), and it falls outside the diagnosis for the genus *Portunites* in several respects. The specimen possesses four frontal teeth, excluding the inner orbital spine, which is true of species of *Portunites*, and possesses four anterolateral spines, excluding the outer orbital spine, which is also characteristic of species of *Portunites*. However, in the specimen of "*P.*" *araucana* Philippi, the four frontal teeth and the inner orbital teeth are approximately the same size, while in species of *Portunites*, the inner orbital spines are smaller than the frontal teeth. The anterolateral teeth in "*P.*" *araucana* are stout at the base, broadly triangular, and are directed forward; anterolateral spine 4 is somewhat less stout but about as long as the other spines. In all *Portunites*, the last anterolateral spine is the longest and stoutest of all the spines, and anterolateral spines 1–3 are directed anterolaterally. The specimen of "*P.*" *araucana* is wider than long, and wider than species of *Portunites*. Finally, the dorsal carapace of the specimen of "*P.*" *araucana* is highly vaulted, especially posteriorly, which is not seen in species of *Portunites*.

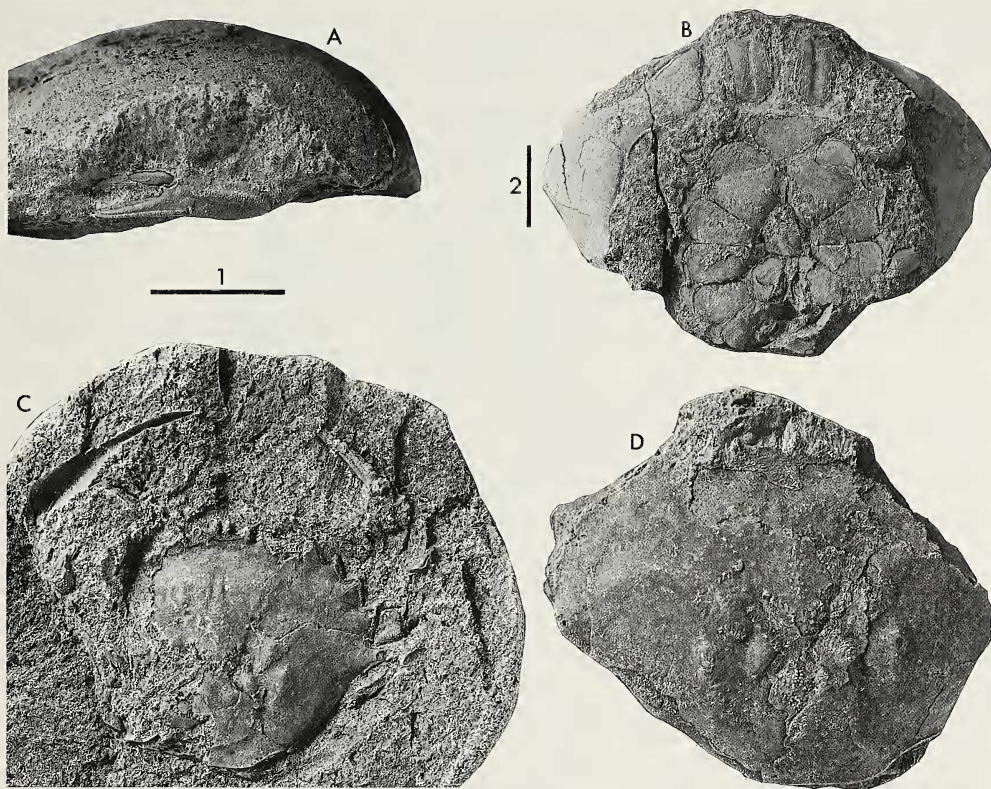


Fig. 8.—*Portunites triangulum* Rathbun. A. Lateral view of outer surface of major cheliped, CM 39669. B. Ventral view, CM 39676. C. Dorsal view of partially preserved carapace, CM 39669. D. Dorsal view of partially preserved carapace, CM 39670. Scale bar 1 for A, C, and D. Scale bar 2 for B. Scale bars = 1 cm.

*Portunites triangulum* Rathbun, 1926  
(Fig. 8, 9)

*Portunites triangulum* Rathbun, 1926:68.

**Diagnosis.**—Portunid with three tubercles arranged in triangular pattern on branchial region just posterior of arcuate ridge; four frontal teeth excluding inner orbital tooth; four sharply triangular anterolateral teeth excluding outer orbital tooth, teeth gradually increasing in size posteriorly; carapace about 70% as long as wide; fronto-orbital margin occupying about 50% maximum carapace width.

**Emendation to Description.**—Carapace somewhat broader than long ( $L/W = 0.70$ ); widest at position of the last and longest lateral spine; posterolateral margins somewhat longer than anterolateral margins; carapace moderately vaulted both transversely and longitudinally; longest lateral spine at midlength; carapace surface finely granular.

Front with four teeth, slightly projected in front of orbits; middle two frontal teeth closely spaced, projected slightly more than outer two frontal teeth; front occupying 23% of the maximum carapace width; orbits directed slightly anterolaterally, upper orbital margin with two fissures, inner fissure much longer and more pronounced than outer fissure; orbits bounded by inner and outer orbital spines, outer orbital spine longer, about as large as first anterolateral spine, directed forward; fronto-orbital margin occupying 50% maximum carapace width. Anterolateral margin with four teeth excluding outer orbital spine, teeth becoming progressively larger posteriorly; first directed forward; second and



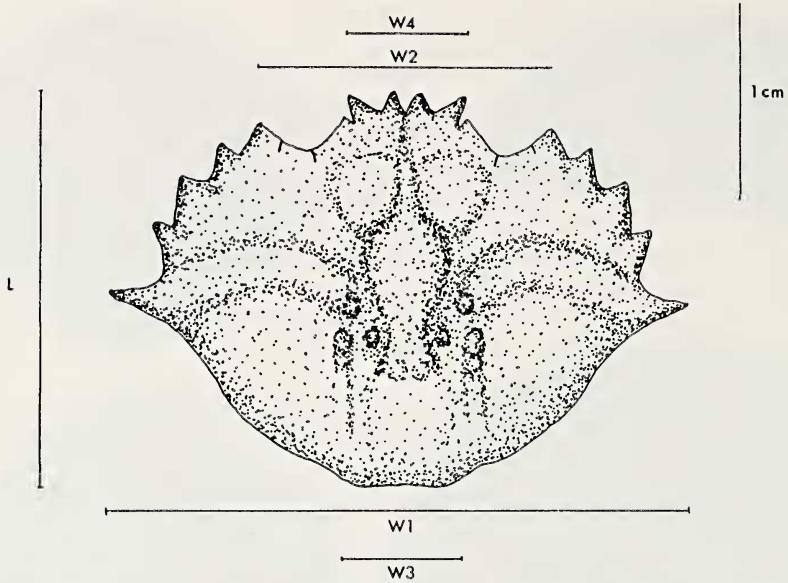


Fig. 9.—Reconstruction of *Portunites triangulum* Rathbun showing the position and orientation of measurements made.

third directed anterolaterally; first through third with slightly concave mesial margins and straight lateral margins; posteriormost longest, narrow, spinelike, directed laterally; posterolateral margin smooth, weakly convex, sinuous; posterior angle broad, concave, rimmed; posterior margin about 33% maximum carapace width, rimmed.

Carapace regions moderately elevated; frontal region slightly sulcate, possessing two low swellings on either side of sulcus, sulcus terminating between two inner frontal teeth; protogastric region tumid posteriorly and flattening near orbital rim; hepatic region slightly inflated; mesogastric region narrow, triangular anteriorly, and widening posteriorly into pentagonal region; cardiac region elevated, with two tubercles; subtle ridge extending in convexly forward arc from lateral spine toward midline, separating cephalic region from the branchial region, terminating in tubercle; mesobranchial region somewhat inflated, bearing three tubercles arranged in triangle pattern near edge of cardiac region, one tubercle of triangle is tubercle at termination of arcuate ridge; metabranchial region with poorly developed longitudinal ridge terminating anteriorly in large tubercle, tubercle included in triangle of tubercles, ridge extending towards posterior margin, gradually disappearing before reaching posterior margin; intestinal region indistinct.

Pterygostomial region finely granular anteriorly, smoother posteriorly; abdomen finely granular anteriorly and smooth posteriorly. Third maxillipeds longer than wide, endognath narrow anteriorly, widening slightly posteriorly, then narrowing and curving abruptly distally into narrow segment attaching to base of appendage; exognath wider than endognath, slightly constricted centrally, upper and lower margins not well known.

Sternum less than 48% maximum carapace width, ovate, narrowest anteriorly, widest at sternite 6, narrowing posteriorly but never as narrow as sternites 1–3; sternites 1–4 fused; sternites 1–3 broadly triangular in shape, apex directed distally, sutures between sternites not evident; sternite 4 petal-shaped, directed anterolaterally, straight axial margin, almost equidimensional, suture between sternites 3 and 4 distinct; sternite 5 petal-shaped, directed anterolaterally, with small peglike projection near lower inner angle; sternite 6 petal-shaped, directed laterally; sternite 7 petal-shaped, directed posterolaterally; sternite 8 poorly known. Sternites 4–7 with episternal projections curving posteriorly, bounding distal margin of next sternite. Abdomen of male extending approximately halfway on sternum, approximately 44% width of sternum, telson triangular, somite 6 about as long as telson but about 1.5 times as wide, remainder of abdomen poorly known.

Chelae unequal; outer surface of manus granular, narrow proximally and widening distally; outer surface with blunt keel extending from proximal margin almost the entire length of manus, keel gradually flattening near distal margin; lower margin of manus rounded, not keeled, granular; upper



Table 5.—Measurements (in mm) taken on the dorsal carapace of specimens of *Portunites triangulum*. W1 = maximum width, W2 = fronto-orbital width, W3 = posterior width, W4 = frontal width, L1 = maximum length.

Specimen number	W1	L1	W2	W3	W4
CM39669	26.4	18.5	13.2	6.2	6.4
CM39670	36.2 <sup>a</sup>	26.6	16.4	13.8	7.9
CM39671	—	—	30.0	—	14.0
CM39672	60.0 <sup>a</sup>	37.9	—	20.1	—
CM39673	45.0 <sup>a</sup>	—	20.4 <sup>a</sup>	—	8.1
CM39676	> 54.0	41.4	—	—	—

<sup>a</sup> Based on half measurements.

margin not well known; distal margin extending from upper to lower margin at about 50° angle, upper part of distal margin with rounded tubercles; inner surface of manus granular, not well known. Fixed finger narrow, long; possessing two keels, one paralleling lower margin and one paralleling upper margin, surface of keels granular, surface between keels and along occlusal surface smoother; occlusal surface armed with several blunt, rounded teeth of varying sizes. Movable finger long, slender, somewhat longer than fixed finger; upper margin granular, not well known; outer surface smoother than upper surface; occlusal surface with several blunt, rounded teeth of varying sizes.

**Measurements.**—See Table 5 for carapace measurements and Table 6 for measurements of chelae. All measurements are in millimeters. Position and orientation of carapace measurements illustrated in Figure 9. CM 39676, W (maximum of sternum) = 27.2, L (maximum of sternum) = 29.5, W (maximum of sixth somite) = 12.0, W (maximum of telson) = 4.7, L (maximum of telson) = 4.1, L (maximum of abdomen) > 15.3.

**Referred Specimens.**—Eight specimens, CM 39669–39676, are deposited in the Carnegie Museum of Natural History.

**Localities and Stratigraphic Position.**—CM 39669–39671 were collected from the RB36 locality. CM 39676 was collected in a concretion from site RB43. A claw fragment, CM 39674 was collected from RB37 as were several flattened specimens—CM 39672, 39673, and 39675. *Portunites triangulum* has also been reported by amateur collectors from sites RB15 and RB18, but these specimens were not seen by the authors.

**Remarks.**—Four of the specimens, CM 39669–39671 and 39676 were preserved in concretions, and all of the specimens retained the carapace cuticle. Several tiny specimens, CM 39675, as well as a claw fragment, CM 39674, were recovered along with other decapods, molluscs, and large amounts of organic material. The material herein described is more complete than that available to Rathbun (1926) when she erected the species *Portunites triangulum*, including a more complete venter and chelipeds, which permits a more complete description of the species.

Table 6.—Measurements (in mm) taken on chelae of specimens of *Portunites triangulum* Rathbun.

Specimen number	L major chela	L upper finger	L minor chela	L upper finger	L lower finger
CM39671	43.8	18.7	38.5	19.9	17.1
CM39669 <sup>a</sup>	14.3	7.3	—	—	—

<sup>a</sup> Assuming preserved chela is major cheliped.

Table 7.—All known species currently referred to *Portunites*.

Taxon	Locality	Age
<i>P. incerta</i> Bell	England/Belgium	early Eocene
<i>P. stintoni</i> Quayle	England	early Eocene
<i>P. sylviae</i> Quayle and Collins	England	late Eocene
<i>P. eocaenica</i> Lörenthey and Beurlen	Hungary	Eocene
<i>P. insculpta</i> Rathbun	North America	mid-Eocene
<i>P. alaskensis</i> Rathbun	North America	Oligocene
<i>P. triangulum</i> Rathbun	North America	Oligocene–early Miocene
<i>P. hexagonalis</i> Nagao	Japan	late Eocene
<i>P. kattachiensis</i> Karasawa	Japan	mid-Eocene

Three species of *Portunites* have previously been described from Washington including *P. alaskensis*, *P. insculpta* Rathbun, and *P. triangulum* (Rathbun, 1926). All were described on the basis of well-preserved carapace material and some chela fragments. *Portunites triangulum* differs from all other species of the genus in bearing a triangular arrangement of tubercles near the axial regions. In addition to lacking a triangle of tubercles on the branchial region, *P. insculpta* has more well-developed carapace regions. Otherwise, *P. insculpta* is the species most similar to *P. triangulum*.

Upon examination of all known species of *Portunites* (Table 7), the main differences between the various species of *Portunites* include differences in the degree of granulation, position of tubercles, definition of carapace regions, and the number, length, and shape of anterolateral spines. Most species possess two orbital fissures in addition to the characters already listed as diagnostic for the genus. Examination of the type species of *Portunites* and all known species historically referred to the genus indicates that it embraces several species that differ in rather substantial aspects from the type species, *P. incerta*. *Portunites kuhni* Bachmayer cannot be retained in the genus because it possesses terraced ornamentation on the dorsal carapace; Karasawa (1991) reported that it belongs to the genus *Liocarcinus* Stimpson. *Portunites subovata* Quayle and Collins lacks the curved ridge separating the cephalic and branchial regions which is a diagnostic character of *Portunites*; this fact alone is sufficient to warrant removal of this taxon from the genus. *Portunites alaskensis*, which has been collected from localities of Oligocene age in Washington, Alaska, and Oregon, possesses a more square carapace and a shorter anterolateral margin than all other species in the genus (Tucker and Feldmann, 1990). The frontal margin of *P. alaskensis* is straighter than in other species of *Portunites*. *Portunites alaskensis* lacks the two orbital fissures common in other members of the genus, and has much larger and much more deeply excavated orbits than other members of the genus. Nagao (1932) observed that *P. hexagonalis* Nagao was most similar to *P. alaskensis*; therefore, in all likelihood, the two species are especially closely related. However, at this time these differences do not warrant removal of the two species from the genus *Portunites*. As has been discussed, *P. triangulum* differs from the type species of *Portunites* in several important features but these differences do not warrant removal of the species from the genus at this time.

All of the known species of *Portunites* have been reported from the Northern Hemisphere (Table 7). Two species from localities in England are early Eocene

in age, suggesting that the genus arose in the early Eocene. Karasawa (1993) suggested that the genus has a Tethyan distributional pattern.

Superfamily Majoidea Samouelle, 1819

Family Majidae Samouelle, 1819

Subfamily Inachinae Alcock, 1895

Genus *Macrocheira* de Haan, 1839

*Type Species*.—*Maja kaempferi* Temminck, 1836.

*Remarks*.—The genus *Macrocheira* was erected by de Haan for one reported extant species, *Macrocheira kaempferi* (Temminck), which is known only from Japan. The genus is placed in the subfamily Inachinae, which is characterized by an overall rounded or pyriform dorsal carapace outline; long, unprotected eye-stalks; long, spindly legs; a single or double rostrum; and poorly developed orbits, sometimes with a pre- and/or postocular spine (Griffin and Tranter, 1986).

Species of the genus *Macrocheira* are characterized by possessing a pyriform carapace; a hepatic spine; spindly legs; a double rostrum; a very poorly developed ocular eave; small pre-, intercalated, and postocular spines; and well-developed carapace regions (Miers, 1886; Rathbun, 1926; Sakai, 1976). The ocular eave and ocular spines are poorly developed and do not afford much protection for the eyestalk, making the orbit fundamentally different than those of the subfamily Majinae, which also have an orbital eave and three orbital spines. The protogastric and mesogastric regions of species of *Macrocheira* are inflated, the metagastric region is depressed, the epi- and mesobranchial regions are inflated, and the metabranchial region is depressed. The urogastric region of species of *Macrocheira* is poorly developed and the cardiac region is oblong and bounded by wide grooves with parallel crenulations positioned oblique to the axis of the grooves. Species of the genus *Macrocheira* are differentiated by the degree of inflation and overall shape of carapace regions, degree and nature of ornamentation on the regions, length of the rostrum, and size of the ocular spines and hepatic spine.

Several Miocene fossil species of *Macrocheira* are known from Japan including *M. ginzaensis* Imaizumi, *M. yabei* (Imaizumi), and *Macrocheira* sp. Imaizumi. *Macrocheira* sp. Karasawa is known from the Pliocene of Japan. One species, *M. teglandi* Rathbun, was previously known from the Oligocene of Washington, USA. The current study includes an emended description of *M. teglandi* from the late Oligocene to early Miocene Pysht Formation. Also described is the new species *Macrocheira longirostra* from the late Eocene Quimper Sandstone of Washington, marking the earliest known occurrence of the genus *Macrocheira*. Fossil species represented by dorsal carapace material, including *M. teglandi*, *M. longirostra*, and *M. yabei*, are considerably smaller than the very large recent species *M. kaempferi* which may attain a maximum width of 305 mm and a maximum length of 335 mm. *Macrocheira kaempferi* has been reported to inhabit bottoms of mud or sand at depths of 50–300 m and is endemic to Japan (Sakai, 1976).

*Macrocheira teglandi* Rathbun, 1926

(Fig. 10, 11)

*Macrocheira teglandi* Rathbun, 1926:148.

*Diagnosis*.—Carapace longer than wide, pyriform; rostrum bifid; carapace tubercles small, acute; regions moderately inflated; protogastric region continuous



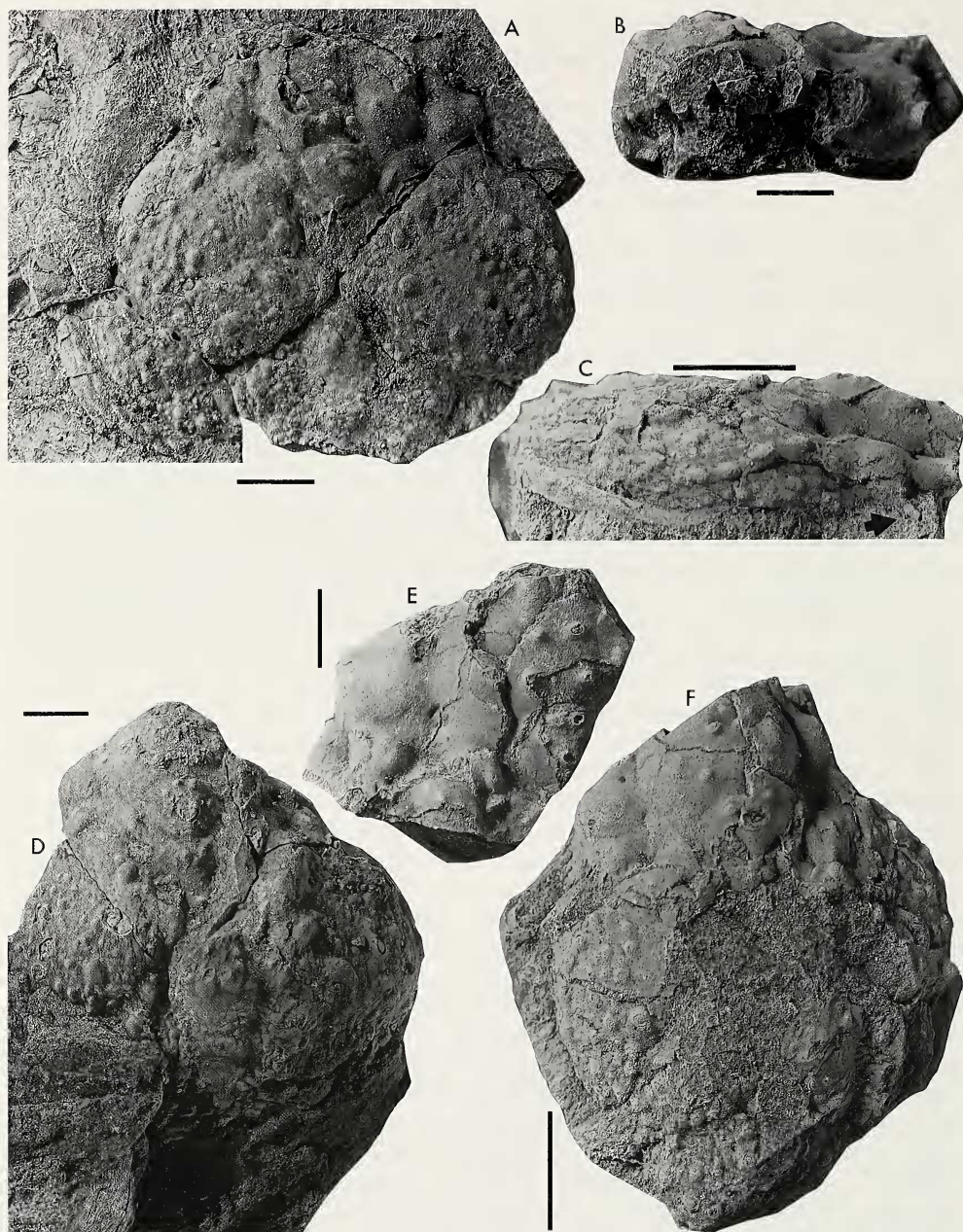


Fig. 10.—*Macrocheira teglandi* Rathbun. A. Dorsal view of partial carapace, CM 39679. B. Frontal view of carapace fragment, CM 39680. Arrow indicates broken base of double rostrum. C. Lateral view of partial carapace, CM 39677. Arrow indicates hepatic spine. D. Dorsal view of carapace fragment, CM 39680. E. Dorsal view of fractured carapace, CM 39678. F. Dorsal view of partial carapace, CM 39677. Scale bars = 1 cm.

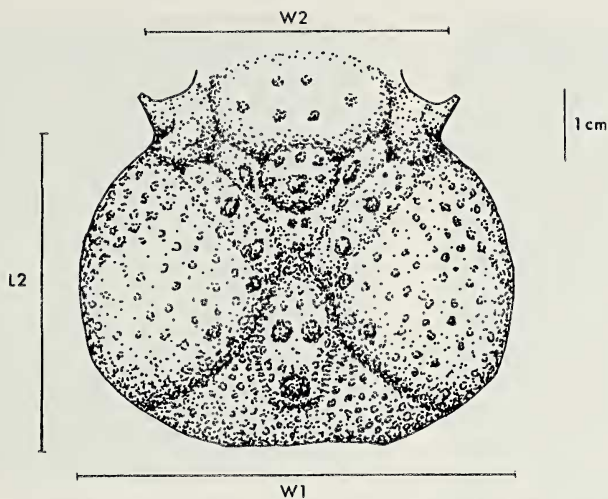


Fig. 11.—Reconstruction of *Macrocheira teglandi* Rathbun showing the position and orientation of measurements made.

unit, broadly subelliptical; hepatic region relatively smooth, with small spine; epi- and mesobranchial regions heavily ornamented, inflated.

*Emendation to Description.*—Carapace pyriform, widest about three-quarters of the distance from the front, vaulted both transversely and longitudinally; surface ornamented with numerous tubercles of varying sizes; regions inflated, bounded by wide, deep grooves.

Front and anterolateral margins poorly known; lateral margins rounded, convex, steep sided; posterior margin nearly straight.

Frontal region poorly known; ornamented with a few tubercles; rostrum bifid, broken at base. Protogastric region inflated; broadly subelliptical; convex proximal margin; concave distal margin; ornamented with several peaked tubercles. Hepatic region inflated; nearly smooth, bearing triangular marginal spine directed anterolaterally. Mesogastric region subelliptical, moderately inflated, bearing several small tubercles along proximal and lateral margins and one prominent tubercle centrally. Metagastric region U-shaped, extending between bases of hepatic regions, widest axially and narrowing distally, ornamented with a few tubercles axially and an oblong tubercle distally. Urogastric region depressed, possessing one central tubercle. Cardiac region elongate, diamond-shaped, ornamented with two broad tubercles anteriorly and large granular tubercle posteriorly, several small tubercles on remainder of region; region bounded by broad grooves with parallel crenulations slightly oblique to axis of groove. Intestinal region flattened, ornamented with numerous small tubercles.

Epibranchial region oblong; separated from metagastric region by broad cervical groove; demarcation between mesobranchial and epibranchial region weakly developed; possessing large tubercle axially; another large tubercle positioned centrally on region; remainder ornamented with small tubercles. Mesobranchial regions large; inflated; steep lateral margins; triangular in shape, apex directed axially; ornamented with numerous small tubercles, some arranged in rows roughly paralleling lateral margin; two large tubercles positioned along axial margin of region. Metabanchial region weakly inflated axially, flattened marginally; triangular in shape; ornamented with numerous small tubercles.

Venter and appendages unknown.

*Measurements.*—Measurements (in millimeters) taken on specimens of *Macrocheira teglandi* are presented in Table 8. Position and orientation of dorsal carapace measurements are illustrated in Figure 11.

*Referred Specimens.*—Specimens referred to *Macrocheira teglandi*, CM 39677–39682, are deposited in the Carnegie Museum of Natural History.

*Localities and Stratigraphic Position.*—Two specimens, CM 39677 and 39678,



Table 8.—Measurements (in mm) taken on four specimens of *Macrocheira teglandi*. W1 = maximum width, L1 = maximum length, W2 = width measured between bases of hepatic spines, L2 = length measured from base of hepatic spine to posterior margin.

Specimen number	Locality	W1	L1	W2	L2
CM39677	RB18	> 34.1	> 45.9	22.2	27.7
CM39680	RB37	—	—	58.8	—
CM39679	RB37	59.7	> 54.0	—	—
CM39678	RB18	65.6	> 69.1	39.8	49.4

were collected from RB18. Three specimens were collected from RB37, including CM 39679 and 39680, as well as CM 39681, a carapace fragment. One carapace fragment was recovered from RB38, CM 39682. Fragments that may be referable to this species were collected at RB36.

*Remarks.*—The material herein referred to *Macrocheira teglandi* includes four broken carapaces. Three of the carapaces lack the front, rostrum, and orbits, and each are fractured in several places; one of these specimens does retain the hepatic spine. The fourth specimen (CM 39680) consists of only a fragment of the anterior portion of the carapace, but it retains the base of the rostrum indicating that it is bifid. Only one of the four specimens confidently referred to *M. teglandi* was preserved in a concretion.

Numerous fractures and the incomplete nature of the specimens herein referred to *Macrocheira teglandi* make recognition of some carapace regions difficult, and the description inherently reflects these deficiencies. Nevertheless, the specimens are confidently referred to *M. teglandi* based upon the overall shape of the carapace, hepatic spine, and shape and ornamentation of the gastric, branchial, cardiac, and intestinal regions of the carapace (see Rathbun, 1926). *Macrocheira teglandi* was named for material possessing the dorsal carapace, venter, and part of a cheliped (Rathbun, 1926). The specimens in this study consist only of dorsal carapace material; however, they are sufficiently well-preserved to allow for a more complete description of the dorsal carapace. The occurrence of *Macrocheira teglandi* in the Pysht Formation does not extend the geologic or geographic range of the species, since Rathbun's holotype was recovered from Tegland Point, a locality that corresponds with locality RB36 of this study.

*Macrocheira teglandi* is most similar to the extant species *M. kaempferi* of Japan, but *M. teglandi* differs from *M. kaempferi* in several respects. The tubercles ornamenting the surface of *M. teglandi* are somewhat larger and more variable in size than those of *M. kaempferi*. The cardiac region of *M. kaempferi* is longer and of an overall different ornamentation than that of *M. teglandi*. The metagastric region of *M. kaempferi* is more depressed and less ornamented than that of *M. teglandi*. The epigastric region of *M. kaempferi* is better developed than that of *M. teglandi*, and *M. kaempferi* is between five and six times as large as *M. teglandi*. *Macrocheira ginzaensis*, *Macrocheira* sp. Imaizumi, and *Macrocheira* sp. Karasawa are known only from claw fragments, making direct comparisons with *M. teglandi* impossible. *Macrocheira yabei* is known from several flattened specimens, so that direct comparison of that species to *M. teglandi* is difficult. *Macrocheira yabei* is longer and narrower than is *M. teglandi* and possesses different ornamentation on the carapace regions than does *M. teglandi*. *Macrocheira teglandi* possesses one spine on the hepatic region, while *M. yabei* possesses two



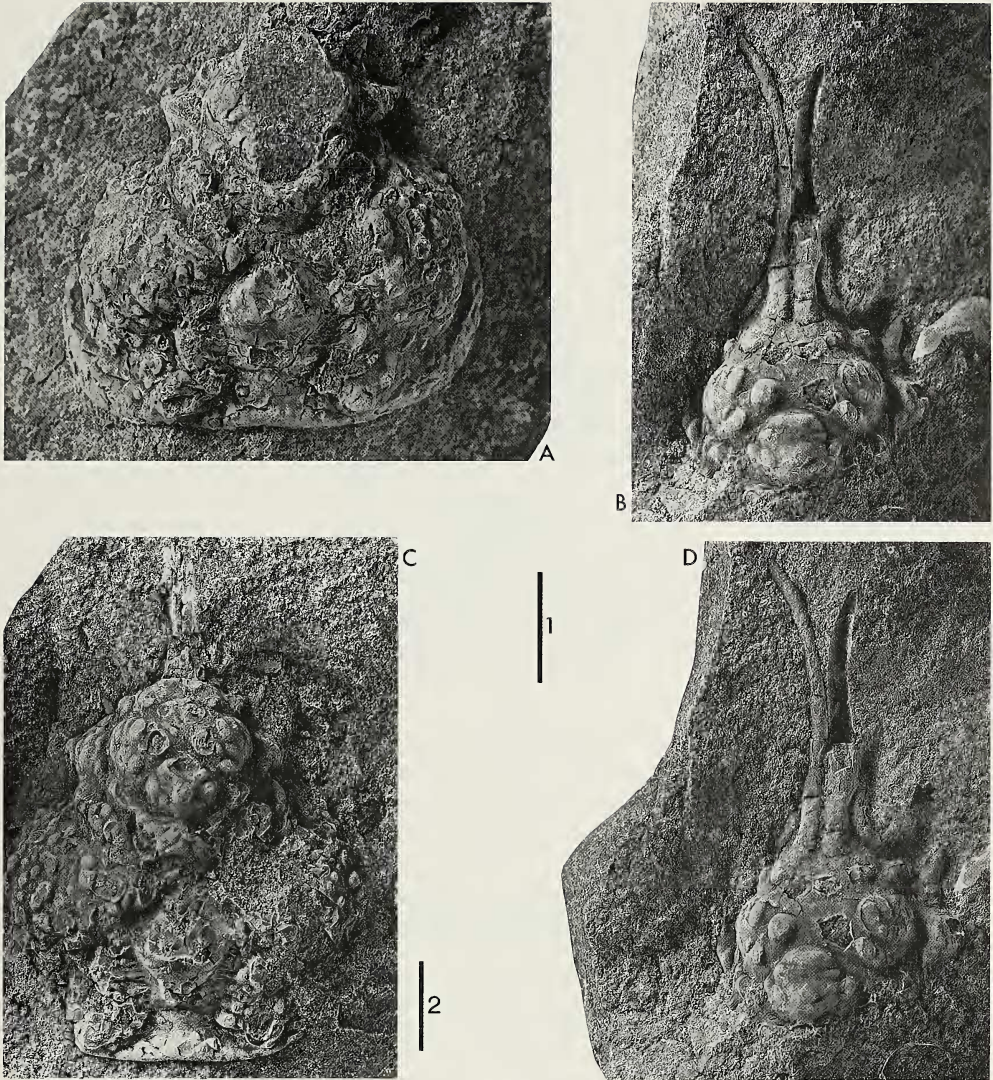


Fig. 12.—*Macrocheira longirostra*. A. Dorsal view of partial carapace, CM 39684. B. Dorsal view of partial specimen, CM 39685. C. Dorsal view of holotype, CM 39683. D. Oblique dorsal view of partial specimen, CM 39685. Arrow indicates preorbital spine on rudimentary ocular eave. Scale bar 1 for A, B, and D. Scale bar 2 for C. Scale bars = 1 cm.

spines on that region. Finally, the branchial regions of *M. teglandi* are more rounded and protrude farther laterally than do those regions of *M. yabei*.

*Macrocheira longirostra*, new species  
(Fig. 12, 13)

**Diagnosis.**—Carapace longer than wide, pyriform; rostrum long, bifid; orbit with narrow eave, antorbital, intercalated, and postorbital spine; carapace regions inflated, bounded by wide grooves; protogastric region composed of two distinct,

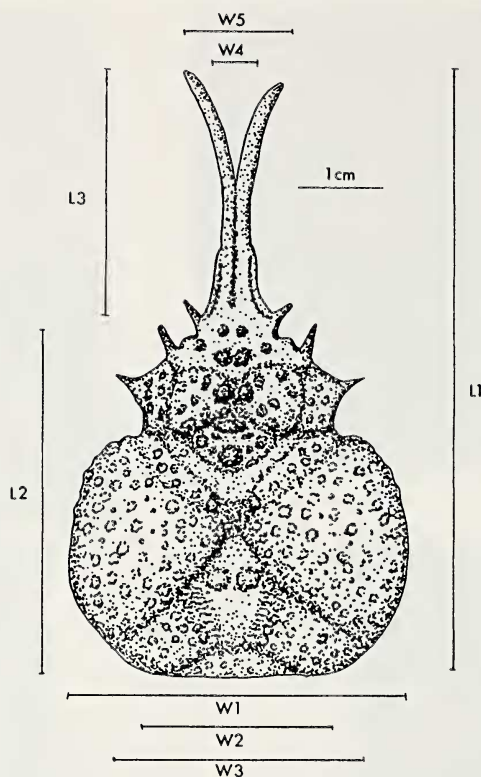


Fig. 13.—Reconstruction of *Macrocheira longirostra* showing the position and orientation of measurements made.

semispherical regions; hepatic region with rounded tubercles and spine; carapace surface ornamented with large, rounded tubercles.

*Description.*—Carapace pyriform, broadest about three-quarters of the distance from the front ( $W/L$  = approximately 0.80), highly vaulted transversely, moderately vaulted longitudinally; possessing inflated regions, regions bounded by broad grooves; surface ornamented with large, smoothly rounded tubercles; lateral margins of branchial regions round, highly convex; posterior margin nearly straight.

Rostrum long, bifid; rostral elements tubular, closely parallel basally, and diverging distally away from center line of carapace.

Ocular eave rudimentary, situated on basal portion of rostrum, eave rimmed, narrow, sinuous outer margin, terminating distally in narrow, attenuated antorbital spine, spine directed anterolaterally; intercalated spine short, blunt, directed more forward than antorbital spine; postorbital spine as long as but more stout than antorbital spine, directed more forward than antorbital spine.

Frontal region ornamented with two tubercles positioned at the outer basal edge of rostrum and two tubercles positioned at inner basal edge of rostrum. Protogastric region subround, inflated so as to be semispherical; ornamented with three large tubercles, round tubercle positioned axially, two oblong tubercles just distal to axial tubercle, several smaller tubercles on remainder of region. Hepatic region inflated, ornamented with several rounded tubercles; possessing rather stout, triangular marginal spine projecting anterolaterally.

Mesogastric region highly inflated, subelliptical, bearing an oblong tubercle centrally and proximally, large tubercle centrally and distally, smaller tubercles on either side of central two tubercles. Metagastric region U-shaped, extending between bases of hepatic regions; widest axially, and narrowest as it approaches margins; region not well known but appearing to be ornamented with numerous tubercles. Urogastric region depressed, not well known. Cardiac region diamond-shaped, inflated, ornamentation not well known but appearing to possess pair of large, rounded tubercles positioned



Table 9.—Measurements (in mm) taken on specimens of *Macrocheira longirostra*. L1 = maximum length, L2 = maximum length (excl. rostrum), L3 = rostral length, W1 = maximum width, W2 = width measured at base of hepatic spine, W3 = width measured between tips of postorbital spines, W4 = rostral width measured at base midway along ocular eave, W5 = width measured between tips of antorbital spines.

Specimen number	L1	L2	L3	W1	W2	W3	W4	W5
CM39683	> 54.6	40.0	> 14.6	> 38.4	23.1	16.1	5.5	11.4 <sup>a</sup>
CM39686	> 40.2	—	> 11.7	> 34.4	23.0 <sup>a</sup>	17.8 <sup>a</sup>	4.8	13.8 <sup>a</sup>
CM39685	—	—	26.6	—	22.0 <sup>a</sup>	18.6 <sup>a</sup>	6.5	13.2 <sup>a</sup>
CM39684	—	38.4	—	39.0	20.7	16.2 <sup>a</sup>	—	—

<sup>a</sup> = based on half measurements.

centrally on either side of the axial line; region delimited by very broad grooves, grooves with parallel crenulations positioned slightly oblique to axis of groove. Intestinal region flattened, broadly trapezoidal, ornamented with a few small tubercles.

Epibranchial region oblong, paralleling metagastric region, widest distally and narrowing axially, ornamented with numerous tubercles, very large tubercle along axial margin of region; separated from metagastric region by broad cervical groove; demarcation between epibranchial regions weakly developed. Mesobranchial region large; broadly triangular, apex of triangle directed axially; ornamented with numerous rounded tubercles of varying size, highly inflated axially, flattening somewhat along margins. Metabranchial region weakly inflated axially and flattened along margins, broadly triangular in shape, bearing several large tubercles along axial margin, remainder of region ornamented with smaller tubercles.

Venter and appendages unknown.

**Measurements.**—Measurements (in millimeters) taken on specimens of *Macrocheira longirostra* are presented in Table 9. Position and orientation of dorsal carapace measurements are illustrated in Figure 13.

**Types.**—The holotype, CM 39683, and three paratypes, CM 39684–39686, are deposited in the Carnegie Museum of Natural History.

**Localities and Stratigraphic Position.**—All of the specimens referred to *Macrocheira longirostra* were collected from site RB40 from the late Eocene Quimper Sandstone.

**Etymology.**—The trivial name is constructed from the Latin word *longus*, meaning long, and the Latin word *rostrum*, meaning beak, bill, snout, or muzzle, in reference to the extremely elongate rostrum exhibited by this species.

**Remarks.**—The material referred to *Macrocheira longirostra* consists solely of specimens preserved in concretions. All of the specimens retain dorsal carapace material, and all consist of dorsal carapaces only, suggesting that they may be molts. Each of the specimens is incomplete, but the preservation of the material is excellent and allows a detailed description of the dorsal carapace to be framed.

The new species, *Macrocheira longirostra*, can be referred to the genus *Macrocheira* based upon possession of several key characters including a pyriform carapace that is longer than wide and a bifid rostrum. The type and sole extant species, *M. kaempferi* possesses a rudimentary orbital eave, antorbital spine, intercalated spine, and postorbital spine. The type species also possesses inflated epi- and mesobranchial regions that are ornamented with numerous tubercles, inflated protogastric regions, an ovoid mesogastric region, a U-shaped metagastric region, a depressed urogastric region, a long, narrow cardiac region, and flattened metabranchial regions. The new species *M. longirostra* possesses all of the above-



listed characters and is therefore referred to the genus *Macrocheira* with confidence.

The new species *Macrocheira longirostra* is congeneric with *M. teglandi* from the Pysht Formation, but is considered to be a distinct species based on several differences. *Macrocheira longirostra* possesses several rounded tubercles on the hepatic region while *M. teglandi* has a nearly smooth hepatic region. The carapace tubercles of *M. longirostra* are more rounded and larger than those of *M. teglandi*, which possesses tubercles that are smaller overall and are more acutely tipped. Carapace regions of *M. longirostra* are more inflated than those of *M. teglandi*. The branchial regions of *M. teglandi* possess smaller, more numerous tubercles, while those regions of *M. longirostra* have fewer, larger tubercles. Finally, the protogastric region of *M. longirostra* is composed of two distinct, rounded regions with several large tubercles while that of *M. teglandi* is a continuous region with smaller, more acute tubercles. Direct comparison of *M. longirostra* with *M. ginzaiensis*, *Macrocheira* sp. Imaizumi, and *Macrocheira* sp. Karasawa is not possible because those three taxa are represented only by claw fragments, which are not present in the *M. longirostra* material. *Macrocheira yabei* was named for tiny, flattened specimens, so direct comparisons with *M. longirostra* are difficult although it appears to be longer and narrower overall than *M. longirostra*. The hepatic region of *M. yabei* was reported to possess two spines; *M. longirostra* possesses only one spine on that region. The branchial regions of *M. yabei* are not as rounded and do not protrude as far laterally as those of *M. longirostra*. Finally, the ornamentation reported for carapace regions of *M. yabei* differs from that seen on regions of *M. longirostra*.

*Macrocheira longirostra* differs from the recent species *M. kaempferi* because *M. longirostra* possesses larger, more rounded tubercles ornamenting the carapace, a shorter cardiac region, and a protogastric region that consists of two distinct, bulbous regions instead of one continuous region such as that of *M. kaempferi*. The hepatic regions of *M. longirostra* are more bulbous and more heavily ornamented than those of *M. kaempferi*. The rostrum of *M. longirostra* is much longer than that of *M. kaempferi*. The rostrum of *M. kaempferi* is quite short in adults, but it has been reported to attain lengths of more than one-half of the carapace length in juveniles (Sakai, 1976). Also, the adults of *M. kaempferi* are much larger than the fossil specimens of *M. longirostra*, at least six times as long based on measurements of *M. kaempferi* given in Sakai (1976). Possibly the fossil specimens are juveniles, but there is no clear indication that this is the case, because all of the specimens referred to the new species are approximately the same size, suggesting that they may be adults. However, each specimen consists only of dorsal carapace material, indicating that they may be molts, perhaps of younger individuals. Only one specimen has a complete rostrum preserved, and this particular specimen consists only of the rostrum, frontal, protogastric, and mesogastric regions. Consequently, it is not possible to compare rostral size with overall size for any of the specimens. Collection of additional fossil specimens will be necessary to determine whether the new species *M. longirostra* exhibits allometric growth in regards to the length of the rostrum and to determine whether the fossil specimens are adults or juveniles.

The occurrence of *Macrocheira longirostra* in the late Eocene rocks of the Quimper Sandstone marks the earliest known occurrence of this genus.

Section Thoracotremata Guinot, 1977  
Superfamily Pinnotheroidea de Haan, 1833  
Family Pinnotheridae de Haan, 1833

*Remarks.*—The specimens herein described superficially resemble members of both the families Pinnotheridae and Hexapodidae, based upon their small size, subrectangular carapace, small orbits, and simple carapace ornamentation. However, the specimens can be referred to the Pinnotheridae based upon several criteria. CM 39688 possesses the abdomen, sternum, and five pereopods. The chelipeds are preserved only as the basal segments; however, pereopods 2–5 are well preserved. Because of the presence of five pereopods, assignment of the material to the Hexapodidae is impossible because that family possesses completely suppressed fifth pereopods (Manning and Holthuis, 1981).

Other criteria support assignment of this material to the Pinnotheridae. Many hexapods, including *Pseudohexapus* Monod, *Parahexapus* Balss, and *Hexapus* de Haan, often have a ridge paralleling the lateral margins; this ridge is not apparent on previously described pinnotherids or the specimens from this study. Members of the Hexapodidae possess a long posterior border, often nearly as long as the widest part of the dorsal carapace. Our specimens possess a posterior border that is only half as long as the maximum carapace width in addition to highly concave posterolateral margins (called posterolateral facets by Sakai [1976]), a characteristic of the subfamily Asthenognathinae of the Pinnotheridae.

Evaluation of the abdomen of CM 39688 is somewhat problematic. The abdomen is more narrow than is typical for females, occupying about half the width of the sternum. However, it is wider than the abdomen of typical males, and possesses rounded lateral margins typical of females. Usually males of both the Hexapodidae and the Pinnotheridae have a straight-sided abdomen. No fusion of any of the abdominal somites is evident in specimen CM 39688. In hexapods, males possess fusion of some of the abdominal somites, often the third through fifth, third and fourth, fifth and sixth, or second through sixth (Manning and Holthuis, 1981). Some pinnotherids also may exhibit fusion of abdominal somites in males (Manning and Holthuis, 1981; Williams, 1984). Neither female hexapods nor female pinnotherids commonly exhibit fusion of any of the somites. Possibly the specimen under study is an immature female due to its rounded lateral margins, lack of fused somites, and intermediate width.

Subfamily Asthenognathinae Stimpson, 1858

*Remarks.*—The material herein described can be confidently referred to the subfamily Asthenognathinae because it possesses an overall trapezoidal dorsal carapace, a carapace that is moderately wider than long, highly concave posterolateral margins, and characteristic shape and arrangement of the carapace regions. The Asthenognathinae contains at least eight genera including *Asthenognathus* Stimpson, known from Japan, the Gulf of Thailand, France, and western Africa, and *Tritodynamia* Ortmann, known from Japan, China, and Korea. One species of *Tritodynamia*, *T. globosa* Karasawa, has been reported from the early–middle Miocene of Japan (Karasawa, 1993), and is herein referred to *Asthenognathus*. *Asthenognathus inaequipes* Stimpson has been reported from Holocene deposits near Osaka Bay, Japan (Schmitt et al., 1973).

Other pinnotherid subfamilies cannot accommodate the specimens described herein. Members of the subfamily Pinnotherinae possess a carapace that is glob-



ular in shape, unlike our specimens, and a carapace that is not wide enough to accommodate the new fossil material. Members of the subfamily Pinnotherellinae possess a broadly transverse carapace which the material studied here does not possess. Additionally, neither of the aforementioned subfamilies can accommodate specimens exhibiting either the trapezoidal shape of the material described herein or its highly concave posterolateral margins. Members of the subfamily Xenophthalminae White possess narrow orbits that are oriented parallel to the axis of the animal and extend posteriorly onto the dorsal carapace (Sakai, 1976), while the specimens of this study have small semicircular orbits.

### Genus *Asthenognathus* Stimpson, 1858

*Type Species.*—*Asthenognathus inaequipes* Stimpson, 1858.

*Remarks.*—The material herein described is referred to the genus *Asthenognathus*. Species of that genus possess a trapezoidal carapace that is not much wider than long, extremely concave posterolateral margins (posterolateral facets of Sakai, 1976), and a weak rim paralleling the posterolateral and posterior margins. Additionally, members of the genus *Asthenognathus* possess a triangular mesogastric region, a small inflated area on the anterior portion of the protogastric region, slightly inflated branchial regions, and a subhexagonal cardiac region. The new specimens possess all of these characters and are therefore referred to that genus.

The Miocene Japanese species *Tritodynamia globosa* Karasawa very closely resembles the new pinnotherid species described below, and it is here referred to the genus *Asthenognathus*. At this time it seems best to assign the new material and the Japanese species to the genus *Asthenognathus* rather than *Tritodynamia* as explained below.

The specimens referred to the new species *Asthenognathus cornishorum* and *A. globosa* (Karasawa) can be differentiated from species of the genus *Tritodynamia* for several reasons. Species of the genus *Tritodynamia* possess a carapace that is wider than long and trapezoidal in shape with posterolateral facets, all characters of the new species and *A. globosa*. However, the shape of the carapace regions of species of *Tritodynamia* is somewhat different than that of the specimens described herein. The cardiac and mesogastric regions are not as well developed in species of *Tritodynamia* as in species of *Asthenognathus* and the new species. The protogastric region is semicircular in shape in species of *Tritodynamia*, while it is subtrapezoidal in species of *Asthenognathus* and the specimens described herein. The dorsal carapace of species of *Tritodynamia* is typically markedly wider than long, while the dorsal carapace of species of the genus *Asthenognathus* and the new species described below is not much wider than long.

Some species have been assigned at various times to both *Asthenognathus* and *Tritodynamia*. For example, *A. atlanticus* Monod has been assigned by some authors to *Tritodynamia*, and many authors have considered *T. japonica* and *A. inaequipes* to be synonymous (Yokoya, 1928; Monod, 1933; Bocquet, 1963, for example). Rathbun (1910) assigned *T. japonica* to *A. japonica*. Bocquet (1963) synonymized the two genera, but the two genera have been kept distinct by all other authors based upon differences between the two genera in the morphology of the third maxilliped (Sakai, 1976).



Fig. 14.—*Asthenognathus cornishorum*. A. Dorsal view of holotype, CM 39687. B. Ventral view, CM 39688. C. Anterior view of holotype, CM 39687. Scale bars = 1 cm.

*Asthenognathus cornishorum*, new species  
(Fig. 14, 15)

**Diagnosis.**—Carapace wider than long, trapezoidal, regions weakly developed, surface finely granular laterally and smoother axially; protogastric region with small swellings anteriorly; orbits small, semi-oval; posterolateral margins highly incurved; row of granules paralleling posterior margin.

**Description.**—Carapace trapezoidal, widening posteriorly, maximum length about 75% the distance from front ( $L/W = 0.71$ ); carapace regions poorly defined; carapace surface finely granular laterally, smoother axially; margins rounded and steep; highly vaulted both longitudinally and transversely.

Frontal margin straight; rostrum deflexed (rostral width/total width = 0.15), sulcate centrally, granular, projecting beyond orbits, distal extreme unknown. Orbits small, semi-oval, weakly rimmed, fronto-orbital width occupying 70% total frontal width. Anterolateral margin diverging distally, steeply rounded; posterolateral margin strongly concave, rimmed, converging distally; posterior margin straight, row of granules paralleling its total length, posterior width/total width = 0.51.

Protogastric region small, granular, small swelling anteriorly along axis, remainder of region weakly inflated, trapezoidal in shape; mesogastric region sulcate anteriorly, smoother than protogastric region, narrow anteriorly and broadening posteriorly into triangular area, bounded on distal margin by well-developed groove, groove interrupted centrally; urogastric region marked only by weakly developed incurved grooves on lateral margin; cardiac region weakly elevated, bounded by very weakly developed grooves, pentagonal in shape with apex directed posteriorly; urogastric and cardiac regions relatively smooth. Remainder of carapace not differentiated into regions.

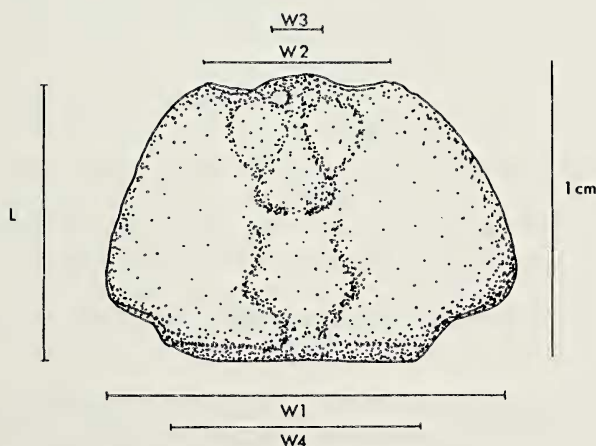


Fig. 15.—Reconstruction of *Asthenognathus cornishorum* showing the position and orientation of measurements made.



Carapace not bilaterally symmetrical, right half more inflated and protruding further laterally than left half.

Sternites 1–4 unknown; sternites 5–8 finely granular. Sternite 5 longer than wide, margins not well known. Sternite 6 wider than long; directed slightly anterolaterally; upper and lower margins straight and nearly parallel; outer margin rounded, with triangular, acutely tipped episternal projection. Sternite 7 similar in size and shape to sternite 6; directed slightly posterolaterally; sternite 8 narrower than 6 and 7; directed posterolaterally; upper margin straight; remainder unknown.

Telson equilaterally triangular; not well known. Somites 3–6 finely granular, with raised, smoother, rounded ridge extending centrally across all four somites; somites widening and becoming shorter distally. Somite 6 trapezoidal in shape; wider than long; upper and lower margins nearly straight and parallel; lateral margins converging proximally. Somite 5 wider than long, widest centrally; upper and lower margins slightly sinuous, nearly parallel; about as long as somite 6 but wider; lateral margins converging slightly proximally. Somite 4 nearly rectangular in shape; lateral margins converging very slightly proximally. Somite 3 rectangular in shape, not well known. Somites 1 and 2 unknown.

Chelipeds and third maxilliped poorly known. Pereiopods 2–4 similar in size and shape. Coxae of pereiopods 2–4 short, equidimensional, tubular. Basis and ischium appearing to be fused, poorly known. Merus of pereiopods 2–4 much longer than high; row of short spines on lower margin. Merus of pereiopod 5 longer than high; sinuous upper and lower margins; narrowing distally; carpus narrow proximally, widening distally, distal margin extending obliquely proximally from upper margin at about 45° angle; propodus longer than high, proximal margin extending obliquely proximally from upper to lower margin at about 45° angle, upper and lower margins appearing to be parallel and straight; remainder of propodus poorly known; dactylus much longer than high, appearing to be lanceolate.

**Measurements.**—All measurements are in millimeters. Position and orientation of dorsal carapace measurements are illustrated in Figure 15. CM 39687, large carapace, L (maximum) = 9.7, W1 (maximum) = 13.6, W2 (fronto-orbital) = 5.2, W3 (rostral) = 2.0, W4 (posterior) = 6.9; small carapace, L (maximum) = 6.9. CM 39689, carapace, L (maximum) = 5.7, W1 (maximum) = 8.5. CM 39688, venter, W (maximum) = 6.1; abdomen, W (maximum) = 2.9, L (maximum) = approximately 2.6; merus of pereiopod 3, L = approximately 2.1; merus of pereiopod 4, L = approximately 3.3; merus of pereiopod 5, L = approximately 3.8.

**Types.**—The holotype, CM 39687, and paratypes, CM 39688 and 39689, are deposited in the Carnegie Museum of Natural History.

**Localities and Stratigraphic Position.**—A concretion bearing two dorsal carapaces (CM 39687) was collected at RB36 and a flattened dorsal carapace (CM 39689) was collected at RB37. The venter, CM 39688, was collected from RB18. All localities are in the Pysht Formation of late Oligocene to early Miocene age.

**Etymology.**—The trivial name honors John and Gloria Cornish of Port Angeles, Washington, who graciously donated fossil material for this study.

**Remarks.**—Two specimens referred to this taxon consist only of dorsal carapaces. Two dorsal carapaces (CM 39687) are preserved in one concretion with one overlapping a portion of the other. The two carapaces retain some of the original carapace material but otherwise are internal molds of the carapace. CM 39689 consists of a flattened dorsal carapace that was recovered from medium-bedded siltstone associated with numerous decapods, molluscs, and a large amount of organic material. CM 39688 consists of a venter and portions of some of the appendages.

*Asthenognathus cornishorum* is most similar to *A. globosa* of the Miocene of Japan (Karasawa, 1992, 1993). *Asthenognathus cornishorum* can be distinguished from *A. globosa* in several ways. *Asthenognathus globosa* has very closely spaced orbits and the fronto-orbital width occupies about 27% of the total carapace width

(Karasawa, 1993). The orbits of *A. cornishorum* are less closely spaced and the fronto-orbital width occupies 38% of the total carapace width. The protogastric region of *A. cornishorum* possesses a small inflated area placed axially in the anteriormost portion of region while *A. globosa* does not. The granules of *A. cornishorum* are proportionately somewhat smaller than those of *A. globosa*. *Asthenognathus globosa* possesses a beaded rim on the posterior margin while *A. cornishorum* has a row of granules paralleling the posterior margin but not forming a rim. The cervical groove of *A. globosa* is better defined than that of *A. cornishorum*.

*Asthenognathus cornishorum* may be distinguished from the recent Japanese species *A. inaequipes* Stimpson because *A. inaequipes* has much more clearly defined carapace regions. *Asthenognathus cornishorum* differs from *A. atlanticus* because *A. atlanticus* possesses more inflated carapace regions than does *A. cornishorum* and a small ridge on the branchial region extending obliquely from the lateral margin toward the posterior margin, which *A. cornishorum* does not possess. *Asthenognathus hexagonum* Rathbun was reported to be strongly hexagonal in shape (Rathbun, 1909), while *A. cornishorum* is trapezoidal in shape.

The dorsal carapace of *Asthenognathus cornishorum* is asymmetrical, because the right half of the dorsal carapace is more inflated and protrudes further laterally than the left side. Interestingly, the dorsal carapaces of two specimens of *A. globosa* figured by Karasawa (1993:pl. 24, fig. 3, 8) also display a similar asymmetry. The asymmetry may be a result of a variety of factors. One possibility is that the crabs were infested by isopods of the family Bopyridae, a common parasite of decapods that causes swelling of the carapace in the area of infestation to accommodate the isopod (Glaessner, 1969; Hessler, 1969; Overstreet, 1983). Bopyrid infestation of decapods is known from as early as the Upper Jurassic and Cretaceous of England, Germany, France, and the former Czechoslovakia (Hessler, 1969). Another possibility is deformation of the dorsal carapace after death either by depositional forces or postdepositional factors such as compression by sediments.

The Recent Japanese species *Asthenognathus inaequipes* Stimpson is free living and inhabits bottoms of mud or sandy mud at depths of 10–65 m (Sakai, 1976). *Asthenognathus atlanticus* Monod is known from the coast of western Africa and France and has been reported to inhabit depths of 8–70 m in the sublittoral zone, at times commensal with tube worms (Monod, 1956; Schmitt et al., 1973). *Asthenognathus hexagonum* Rathbun was collected from the Gulf of Siam in mud at a depth of 15 m (Rathbun, 1909).

Assignment of the new material and the Japanese species to the genus *Asthenognathus* marks the first notice of the genus in the fossil record and one of the earliest known occurrences. The Japanese species *A. globosa* is known from the early Miocene of Japan, so the two species are of approximately the same age, with the Pysht specimens most likely being slightly older.

## DISCUSSION

### General

The decapod assemblage recovered from the Pysht Formation and the Quimper Sandstone can be used to help corroborate the previously reported depths and depositional environments for those formations. Taphonomy of the decapod specimens provides insight into conditions in the depositional area while the two



formations were being deposited. Most importantly, the decapod fauna provides new evidence of a strong affinity between the late Eocene to early Miocene decapod fauna from the Pacific Northwest and the Cenozoic decapod fauna reported from Japan. Additionally, several species of the Pysht Formation and the Quimper Sandstone have modern congeners in the Pacific Ocean. The remarkable similarity of the Japanese and American faunas suggests that a distinct decapod fauna developed in the North Pacific as early as the late Eocene and that faunal exchange between the two areas was significant and may have continued until relatively recently.

### *Taphonomy of Pysht Formation Decapods*

The decapod specimens of the Pysht Formation are almost all well preserved, although some specimens are fragmented or broken. In almost all cases, the cuticle of the specimens is present and well preserved. Some specimens appear to be corpses, including individuals of *Portunites triangulum*, *Mursia marcusana*, and *Asthenognathus cornishorum*, because they possess either the abdomen or both the abdomen and chelipeds. All other decapod specimens consist of portions of, or entire, carapaces or cheliped fragments, suggesting that the majority of the specimens may be molts. The excellent preservation of the thalassinoids, especially *Callianopsis clallamensis*, suggests minimal reworking of the specimens in the depositional environment. Some specimens of *C. clallamensis* possess a well-preserved carapace, abdominal somites, and large portions of both the major and minor chelipeds, which is unusual in the fossil record because only the relatively well-calcified chelae of thalassinoids are commonly preserved. The excellent preservation of the venter and appendages of *A. cornishorum*, *P. triangulum*, and *M. marcusana* supports the suggestion that the fossils experienced little reworking by depositional processes. Other supporting evidence includes one carapace of *Trichopeltarion berglundorum* and two carapaces of *M. marcusana* which are extremely well preserved, including nearly complete lateral spines and carapace morphology. Associated pelecypods are often articulated and gastropods are commonly unbroken.

However, several factors suggest that there was at least some degree of reworking and possible mixing of faunas in the depositional environment. Two specimens of *Mursia marcusana* and one specimen of *Trichopeltarion berglundorum* are preserved only as carapace fragments. Several specimens of *Portunites triangulum* are preserved as carapace fragments, and all of the specimens of *Macrocheira teglandi* are preserved as carapace fragments or broken carapaces. Many specimens of *Callianopsis clallamensis* and most of the other thalassinoid specimens are broken or incomplete. In some cases, associated pelecypods were broken or disarticulated and gastropods sometimes were broken, especially at the apex or near the aperture.

Additionally, many concretions, especially those collected from the RB18 locality, contain large quantities of dispersed organic material appearing to be mainly plant remains. This suggests that there were at least periodic influxes of organic matter from nearshore environments. The RB37 locality was the site of recovery of large blocks of siltstone that contain numerous decapods and molluscs and a large amount of organic material, mostly wood and leaves. Decapods, including *Portunites triangulum*, *Mursia marcusana*, and *Asthenognathus cornishorum*, and molluscs collected from this siltstone are preserved on bedding planes, flattened,

and in some cases are crushed. Also preserved in the siltstone are a large number of what appear to be juvenile decapods, possibly of the species *Portunites triangulum*. The siltstone occurred as float in the intertidal zone, so it is not positive that the blocks originated in the Pysht Formation. However, several factors indicate that they did. First, the blocks contain decapods that are similar to those collected from other Pysht Formation localities. Second, the blocks contain large quantities of plant material and organic matter, and similar material is found at other localities of the Pysht Formation, albeit in smaller quantities. Third, the blocks are composed of well-indurated grey siltstone, and the other Pysht localities also contain grey siltstone, although it is less well-indurated. The siltstone blocks could represent a storm deposit, including a mix of plant material from nearshore environments and decapods and molluscs from both shallow- and deep-water environments.

Since the Pysht Formation contains evidence of quiet-water depositional conditions as well as evidence of some reworking of specimens, it is quite possible that elements of both conditions existed during Pysht Formation deposition. Possibly the depositional environment was primarily quiet with moderately rapid sedimentation, which is characteristic of steep and tectonically active continental slopes such as the northwest coast of North America. The excellent preservation of the carapace material of some of the decapod specimens suggests rapid sedimentation in the depositional area facilitating rapid burial of specimens. This could account for well-preserved decapod specimens. Periodic storm, seismic, or other catastrophic events could account for fragmentation of some decapod specimens and for deposits composed of large quantities of organic material and flattened decapods and molluscs. Periodic catastrophic events could also have facilitated downslope mixing of shallow- and deep-water fauna, thus accounting for the presence of species of the shallow-water genus *Asthenognathus* with a preponderance of species of deep-water genera such as *Callianopsis*, *Trichopeltarion*, *Mursia*, and *Macrocheira*.

*Callianopsis clallamensis* is by far the most abundant taxon of the decapod fauna of the Pysht Formation, with more than 90 individuals of that species having been collected (Hopkins and Feldmann, 1997). Relative abundances of decapod taxa could be related to preservation potential of each decapod taxon; however, note that thalassinoideans such as *C. clallamensis* are typically poorly preserved. It is likely that this taxon was both abundant and living under conditions favorable for excellent preservation. The burrowing habit of thalassinoideans would likely improve preservation potential of both molts and corpses, especially if the depositional area received large amounts of sedimentation to quickly fill and bury burrows. Since burial of the carapace would essentially be accomplished immediately after molting or death, it would be likely that specimens could be extremely well preserved and in great quantity. This is the case with the material in this study. Numerous burrows were observed in outcrops of the Pysht Formation, aligned both horizontally and vertically with respect to bedding, and some burrows were observed to contain fragments of thalassinoideans. However, most of the decapods were preserved in concretions, not burrows.

Other decapod taxa are represented by far fewer specimens. For instance, *Trichopeltarion berglundorum* is known from only two specimens and *Asthenognathus cornishorum* from only three. *Portunites triangulum* is known from eight specimens in addition to numerous tiny specimens that appear to be juveniles preserved on a bedding plane of siltstone associated with large quantities of or-



Table 10.—*Bathymetric range for Recent genera that have fossil representatives in the Pysht Formation and Quimper Sandstone.*

Decapod taxa	Depth in meters
<i>Callianopsis</i> sp.	350–650
<i>Mursia</i> spp.	25–730
<i>Trichopeltarion</i> spp.	0–1650
<i>Macrocheira</i> sp.	50–300
<i>Asthenognathus</i> spp.	8–70

ganic material. All other decapod taxa from the Pysht Formation are known from ten or fewer specimens. It is plausible that decapods other than *Callianopsis clallamensis* inhabited areas of the open shelf that were not necessarily conducive to rapid burial of corpses or molts and were therefore less often preserved. Specimens could have been disarticulated, swept away by currents, or ingested by scavengers before burial could occur. Probable swimmers, such as *Portunites triangulum*, would have likely inhabited more open water environments than thalassinoids, which would have decreased their relative preservation potential. It is also possible that the relative abundances of the other decapod taxa preserved in the Pysht Formation were simply much lower than that of *C. clallamensis*.

#### *Taphonomy of Quimper Sandstone Decapods*

Specimens of *Macrocheira longirostra* consist only of carapaces, suggesting that they are molts. The cuticle is extremely well preserved, and all specimens are preserved in concretions, but all of the specimens are broken. This suggests that the specimens experienced at least some reworking during or after deposition. The Quimper Sandstone has been reported to have been initially deposited in a shallow-water, high-energy environment that subsequently deepened, resulting in deposition below wave base (Babcock et al., 1994). It is unknown whether the specimens were collected in the lower or upper part of the Quimper Sandstone; however, either condition could easily result in reworked fossil specimens. In either case, the taphonomy of the fossils does not suggest depositional conditions different than those previously reported for the Quimper Sandstone.

#### *Bathymetry of the Pysht Formation*

The bathymetric ranges for extant genera with congeners in the Pysht Formation show that the depositional environment of the Pysht Formation was more likely to be moderately deep than shallow (Table 10). The depth ranges for *Mursia* (Table 3), *Trichopeltarion* (Table 4), and *Macrocheira* overlap between depths of 50–300 m. The two genera *Callianopsis* and *Asthenognathus* fall outside of this range. The sole modern species of *Callianopsis* is found at depths of 350–650 m, slightly deeper than the 50–300 m range. Modern species of *Asthenognathus* inhabit a depth range of 8–70 m, which overlaps the shallow end of the range for *Mursia*, *Trichopeltarion*, and *Macrocheira*. However, the preponderance of the evidence corroborates the depth previously reported for the Pysht Formation. As has been discussed, mollusc and foraminiferal assemblages indicate that the Pysht Formation was initially deposited at bathyal depths of 300–1830 m (Rau, 1964), and subsequently shallowed to inner sublittoral depths, probably an outer-shelf environment, near the end of deposition of the formation (Addicott, 1976). The

only genus that does not support this conclusion is *Asthenognathus*, species of which currently inhabit shallow-water inner- to middle-shelf environments. It is possible that this genus inhabited deeper waters in the past, rendering comparison with modern congeners inappropriate. It is also possible that the occurrence of *Asthenognathus* is a result of downslope mixing of a shallower-water taxon with deep-water taxa. It is more likely that the shallow-water genus *Asthenognathus* would be mixed with deeper-water genera as a result of downslope mixing than is a scenario where the deeper-water genus *Callianopsis* would be mixed with shallower-water genera, unless all the genera were washed downslope to the depth at which *Callianopsis* lived.

### *Bathymetry of the Quimper Sandstone*

The depositional environment of the Quimper Sandstone is believed to initially have been an inner shelf in "upper sublittoral to sublittoral" conditions (Durham, 1942, 1944; Armentrout and Berta, 1977:225) that subsequently deepened to "sublittoral to upper bathyal depths" (Armentrout and Berta, 1977:225). The decapod species from this formation, *Macrocheira longirostra*, has a modern congener that inhabits depths of 50–300 m, which corroborates the previously reported depth for the Quimper Sandstone.

### *Paleobiogeography*

Five of the decapod species of the Pysht Formation, including *Callianopsis clallamensis*, *Mursia marcusana*, *Trichopeltarion berglundorum*, *Macrocheira longirostra*, and *Asthenognathus cornishorum*, have Recent congeners that are known primarily or exclusively from the Pacific Ocean. Two species of presumably extinct genera of the Pysht Formation, including *Callianassa* sensu lato cf. *C. porterensis* and *Callianassa* sensu lato sp. 2 are known only from that formation, and one species, *Portunites triangulum*, is from an extinct genus known from both the Atlantic and Pacific oceans. The decapod from the Quimper Sandstone is known only from the Pacific Ocean. Three of the species from the Pysht Formation are members of genera that have been reported from high middle latitudes, including *Portunites*, *Macrocheira*, and *Callianopsis*. The genera *Trichopeltarion*, *Mursia*, and *Asthenognathus* are known from tropical, subtropical, and middle latitudes.

Five of the species herein described from the Pysht Formation were previously known from Oligocene rocks of Washington, including *Callianopsis clallamensis*, *Callianassa* sensu lato cf. *C. porterensis*, *Mursia marcusana*, *Portunites triangulum*, and *Macrocheira teglandi* (Rathbun, 1926). *Asthenognathus* was previously unknown from the Pacific Coast of North America, and only one extant species of *Trichopeltarion* was previously known from the Pacific Coast of North America. The genus *Macrocheira* was not previously known from the Quimper Sandstone. The species *Callianassa* sensu lato sp. 2 was not previously known from the Pacific Coast of North America, but it is not possible to comment on generic distribution of this species since generic placement of the species is unknown at this time.

The sole extant species of the genus *Callianopsis* is known from the west coast of North America from Alaska to Baja California (Rathbun, 1902). Fossil species are known from the upper Eocene to lower Oligocene and early to early middle Miocene of Japan (Karasawa, 1993; Kato and Karasawa, 1994). The species *Cal-*



*lianopsis clallamensis* (Withers) has been reported from the late Oligocene to early Miocene Pysht Formation of northwestern Washington (Hopkins and Feldmann, 1997). It seems reasonable to suggest that the genus arose in the Eocene, perhaps in the western Pacific, and was subsequently dispersed to other North Pacific localities.

Two genera from the Pysht Formation, *Mursia* and *Trichopeltarion*, are cosmopolitan in distribution (Tables 3 and 4, respectively). The earliest known occurrences of both genera are from Pacific localities. Three species of *Mursia* are known from the Oligocene and several Miocene species have been reported from central Europe and Japan (Table 3). It appears that this genus may have arisen in the eastern Pacific during the Oligocene and was subsequently dispersed to its current range (Table 3). Faunal exchange between the Pacific and Atlantic oceans could have occurred through the incomplete isthmus connecting North and South America until three to five million years ago (Briggs, 1987), accounting for dispersal of the genus into the Atlantic Ocean.

The genus *Trichopeltarion* is herein reported from the late Oligocene to early Miocene Pysht Formation. Other fossil species have been reported from Miocene deposits of Japan, Fiji, and New Zealand (Table 4). At this time it is not possible to comment on whether or not the new species of *Trichopeltarion* recovered from the Pysht Formation is the earliest known occurrence of that genus, because detailed and accurate stratigraphy and age of the collecting localities of *T. berglundorum* in the Pysht Formation are currently unknown. It appears that the genus arose during the Oligocene in the Pacific and was subsequently distributed to its current range throughout the entire Pacific and Indian oceans as well as localities in the Atlantic Ocean. As mentioned, faunal exchange between the Pacific and Atlantic oceans could have occurred through the incomplete Isthmus of Panama, accounting for the presence of species of *Trichopeltarion* in the Gulf of Mexico and Ivory Coast on the west coast of Africa.

The genus *Portunites* appears to have arisen in the early Eocene and interestingly, all occurrences of the genus are from high middle latitudes of the Northern Hemisphere (Table 7). Karasawa (1993) suggested that the genus has a Tethyan distribution. If this were the case, occurrences would be expected from Asia, India, South Pacific islands, and China, and confirmation of that hypothesis must await collection of more fossil material. Since species of the genus are currently known only from high middle latitudes, it might be expected that species of *Portunites* recovered from Tethyan areas would inhabit deep, cool water since the Tethys is closer to the subtropics than the localities at which species of the genus have previously been collected.

The new species *Macrocheira longirostra* marks the earliest known occurrence of the genus, having been collected from the late Eocene Quimper Sandstone. This suggests that the genus may have arisen in the Eocene in the eastern Pacific and been dispersed subsequently across the Pacific to Japan, where the sole extant species is currently found. Species of this genus, in addition to *Portunites*, are known solely from high middle latitude localities in the Northern Hemisphere, suggesting that species of the genus may have had difficulty surviving equatorial conditions during east-west dispersal in the Pacific Ocean unless they inhabited extremely deep environments. West-east dispersal of the genus would accommodate its apparent preference for high middle latitudes in the North Pacific, but the fossil record does not support this hypothesis at this time.

The genus *Asthenognathus* is known from Recent localities in France, Japan,

## EARLY MIOCENE 20 Ma

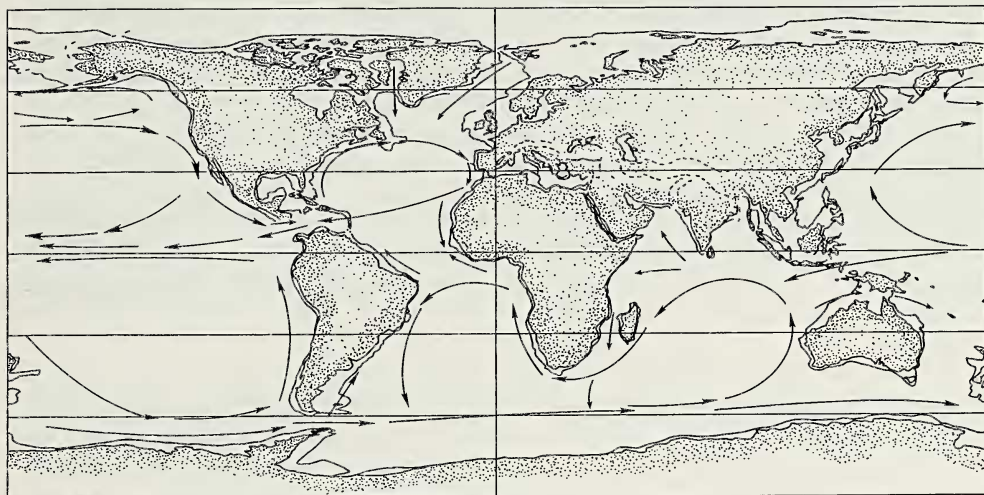


Fig. 16.—Paleocirculation patterns for the late Oligocene depicted on an early Miocene map. Circulation patterns from B. U. Haq in J. P. Kennett (1982:726, fig. 19–16).

the Gulf of Siam, and the coast of northwest Africa. The latter two localities are near the subtropics, as opposed to many other decapod genera reported from the Pysht Formation which are known from high middle latitudes. The species referred here to *Asthenognathus* marks one of the earliest known occurrences of it with another species known from the Miocene of Japan. It seems reasonable to suggest that the genus may have arisen during the late Oligocene or early Miocene in the northeastern Pacific and subsequently been distributed, perhaps along equatorial currents, to localities in the southern Pacific and Japan. The genus could have been distributed to the Atlantic through the incomplete Isthmus of Panama or from the Indian Ocean around the southern tip of Africa to its Recent localities along the coast of northwest Africa. Alternatively, the genus may have arisen in the western Pacific and been subsequently dispersed to North America and other localities.

Perhaps the most important aspect of the assemblage of decapods of the Pysht Formation is the striking affinity with the Miocene decapod fauna of Japan. Every decapod species described from the Pysht Formation, with the exception of *Callianassa* sensu lato cf. *C. porterensis* and *Callianassa* sensu lato sp. 2. Five of the decapod taxa described from the Pysht Formation have extant congeners in the Pacific Ocean. This suggests that decapods were being freely dispersed between the east and west Pacific at least as early as the middle Tertiary and that evidence of this dispersal is preserved in the Recent fauna.

The similarity between the decapod fauna of the Pysht Formation and that of the Cenozoic of Japan suggests that a distinctive North Pacific decapod fauna developed as early as the late Eocene (Fig. 16). Decapod faunal affinities of Cretaceous and Paleogene localities in the Southern Hemisphere, including Antarctica, South America, and New Zealand, have been discussed by Feldmann et al. (1995), and it appears that broad faunal affinities also existed in the North Pacific as well. For example, faunal affinities exist between the middle Eocene



Manda Group decapod fauna of Japan and the lower Tertiary decapod fauna of Prince William Sound, Alaska. The genera *Raninoides*, *Portunites*, and *Branchioplax* each have species present in both faunas. In addition, the Eocene Hoko River Formation, which is part of the Twin River Group, possesses decapod genera including raninids and goneplacids, which may upon further study provide evidence of faunal similarity between the Japanese decapod fauna and the North American decapod fauna (Tucker, personal communication).

The Cenozoic decapod fauna described from Japan appears to be more diverse in terms of numbers of genera and species than the Cenozoic decapod fauna of the Northwest Coast of North America. However, research on currently unstudied specimens of the Twin River Group and other formations from Washington and Oregon may change that interpretation in the future (Tucker, personal communication).

Two of the species described from the Pysht Formation, *Macrocheira teglandi* and *Asthenognathus cornishorum*, have extant congeners inhabiting Japan but not the Pacific Coast of North America. *Mursia marcusana* and *Trichopeltarion berglundorum*, have extant congeners in both Japan and the Pacific Coast of North America. However, note that the apparent closest living relative of *M. marcusana*, *M. armata*, inhabits the seas of Japan. *Callianopsis clallamensis* has a recent congener from the Pacific Coast of North America and not Japan. Several possibilities for explaining this phenomenon exist. Perhaps the coast of Japan currently provides an environment more tolerable today for species of some genera found in the Pysht Formation than does the modern Pacific Coast of North America. Fossil species of Pysht genera may have originated in the eastern Pacific and been subsequently dispersed to Japan, where they were better able to thrive into the Recent. Conversely, fossil species may have originated in Japan and been dispersed to the eastern Pacific, where they lived until conditions became unsuitable. In the case of *Callianopsis*, it appears that the depositional environment of the Pysht Formation, a deep, cool continental shelf or slope, is almost identical to environments that the modern species now inhabits.

#### SUMMARY AND CONCLUSIONS

This study of the decapod fauna of the Pysht Formation first mentioned in 1926 by Rathbun has resulted in emended descriptions for four previously described taxa, *Mursia marcusana*, *Macrocheira teglandi*, *Portunites triangulum*, and *Callianassa* cf. *C. porterensis*, and descriptions of three previously undescribed taxa, *Trichopeltarion berglundorum*, *Asthenognathus cornishorum*, and *Callianassa* sensu lato sp. 2. One new decapod species from the Quimper Sandstone has been described, *Macrocheira longirostra*. The lower part of the Pysht Formation has been reported to have been deposited at depths of 300–1830 m but subsequently shallowed to inner sublittoral depths, and the Quimper Sandstone has been reported to have been initially deposited in littoral to sublittoral conditions that subsequently deepened to sublittoral to upper bathyal depths. Environmental and depth information on extant congeners of decapods from both the Pysht Formation and the Quimper Sandstone corroborate the previously reported depth and depositional environments for both formations.

The decapod fauna of the Pysht Formation and the Quimper Sandstone is remarkably similar to the decapod fauna of the Cenozoic of Japan. That similarity, along with the fact that five of the decapod species of the Pysht Formation have

Recent congeners in the Pacific Ocean, suggests that a distinctive decapod fauna developed in the North Pacific Ocean as early as the late Eocene and that evidence of this fauna persists into Recent times.

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